

Some Discrete Competition Models and the Competitive Exclusion Principle[†]

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(Received 6 May 2003; In final form 11 November 2003)

Dedicated to Professor Saber Elaydi on the Occasion of His 60th Birthday

A difference equation model, called the Leslie/Gower model, played a key historical role in laboratory experiments that helped establish the “competitive exclusion principle” in ecology. We show that this model has the same dynamic scenarios as the famous Lotka/Volterra (differential equation) competition model. It is less well known that some anomalous results from the experiments seem to contradict the exclusion principle and Lotka/Volterra dynamics. We give an example of a competition model that has non-Lotka/Volterra dynamics that are consistent with the anomalous case.

Keywords: Difference equations; Global stability; Competition models; Competitive exclusion principle; Leslie/Gower model; Lotka/Volterra dynamics

AMS Nos: 39A11; 92D40

INTRODUCTION

A fundamental tenet in theoretical ecology is the “competitive exclusion principle”. According to this tenet, two similar species competing for a limited resource cannot coexist; one of the species will be driven to extinction. This principle is supported by many mathematical models, the most famous of which is the Lotka/Volterra differential equation model for two competing species. It is well known that the Lotka/Volterra model allows just four dynamic scenarios, all of which involve only equilibria as possible asymptotic states. A coexistence case (in the form of a globally asymptotically stable equilibrium) occurs if the competition between the species is weak. If, however, the inter-species competition is sufficiently strong, then competitive exclusion occurs (in the form of an equilibrium state possessing one zero component). The competitive exclusion case has three possible dynamic scenarios, depending upon relationships among the model coefficients. Two of these scenarios are symmetric cases that have globally attracting equilibria in which one species is absent. The third, and final scenario, has an unstable (saddle) coexistence

[†]This research was supported by National Science Foundation grant DMS 9973126.

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equilibrium whose stable manifold determines two basins of attraction, one for each of the competitive exclusion equilibria. In this “saddle” case, the species that goes extinct is determined by the initial conditions of both species.

During the 1940s, 50s and 60s, laboratory experiments played a key role in establishing the competitive exclusion principle in theoretical ecology. One series of laboratory studies, which today is still cited in text books, was conducted by Park and Mertz using two species of flour beetles (of the genus *Tribolium*) [37–40]. Park and his collaborators, Leslie and Gower, used a difference equation model in these studies, rather than the Lotka/Volterra differential equations [26]. Although they did not give a mathematical analysis of their model, they worked under the assumption that it possesses the same dynamic scenarios as the Lotka/Volterra model.

It is interesting that although Park’s experiments were considered a validation of the competitive exclusion principle, there were some anomalous results. In one experiment competitive exclusion did not always occur. Whether competitive coexistence occurred or competitive exclusion occurred (and how) depended on the initial population numbers given the two species. This result puzzled Park and his collaborators, since this dynamic scenario is not allowed by Lotka/Volterra-type competition models which guided their thinking [14,27]. A natural question to examine, from a mathematical point of view, is whether or not there exist any two species competition models that allow for such a multiple attractor, coexistence/exclusion case. A number of studies involving competition models have, under certain circumstances, found results of non-Lotka/Volterra type or that contradicted the competitive exclusion principle in one way or another [2,5–8,10,13,20,22–24,28,29,31–36,41,42]. None of these results, however, involve the multiple attractor scenario described above.

The Leslie/Gower competition model was studied by Liu and Elaydi, who showed that all bounded orbits converge to an equilibrium in an eventually monotonic manner (using the theory of discrete monotone flows) [30]. In this paper we will extend this result by showing that the Leslie/Gower model has the same dynamic scenarios as the Lotka/Volterra model (characterizing these cases according to model parameters). We will also investigate a competition model that does conform not to the Lotka/Volterra cases and that allows for multiple, coexistence and exclusion, attractors.

THE LESLIE/GOWER MODEL

If $b > 1$ all solutions of the Beverton/Holt equation

$$x_{t+1} = b \frac{1}{1 + c_{11}x_t} x_t$$

with $x_0 > 0$ tend (monotonically) to the equilibrium $x = (b - 1)/c_{11}$. This difference equation is an appropriate analog of the logistic differential equation [12]. Just as the famous Lotka/Volterra two species (differential equation) competition model is a modification of the logistic differential equation, the Leslie/Gower (difference equation) competition model [26]

$$x_{t+1} = b_1 \frac{1}{1 + c_{11}x_t + c_{12}y_t} x_t$$

$$y_{t+1} = b_2 \frac{1}{1 + c_{21}x_t + c_{22}y_t} y_t$$

is a modification of the Beverton/Holt equation. In this model all coefficients are positive and we can therefore scale x and y so that $c_{11} = c_{22} = 1$. Without loss in generality we consider

the system

$$x_{t+1} = b_1 \frac{1}{1 + x_t + c_1 y_t} x_t \tag{1}$$

$$y_{t+1} = b_2 \frac{1}{1 + c_2 x_t + y_t} y_t \tag{2}$$

where $b_i > 0$ and $c_i > 0$. We denote solutions of this system by (x_t, y_t) , $t = 0, 1, 2, 3, \dots$ (For some results concerning difference equations defined by rational functions see Refs. [3,4,25]. The results in these papers do not apply to the Leslie/Gower model, however. Other papers that deal with discrete competition models include [16–19].)

In population dynamic applications we are interested in solutions with non-negative components $x_t \geq 0, y_t \geq 0$. Let $R_+^2 \doteq [0, +\infty) \times [0, +\infty)$ and $\mathring{R}_+^2 \doteq (0, +\infty) \times (0, +\infty)$

$$\phi : (x, y) \rightarrow \left(b_1 \frac{1}{1 + x + c_1 y} x, \quad b_2 \frac{1}{1 + c_2 x + y} y \right)$$

takes R_+^2 into itself. The same is true of \mathring{R}_+^2 and of the coordinate axes $[0, +\infty) \times \{0\}$ and $\{0\} \times [0, +\infty)$. Moreover, all solutions in R_+^2 are forward bounded. Specifically, $\phi : R_+^2 \rightarrow S \doteq [0, b_1) \times [0, b_2)$. It follows from Proposition 1 in Ref. [30] that all orbits in R_+^2 approach an equilibrium as $t \rightarrow +\infty$.

The map ϕ is also invertible on R_+^2 , since for $(x', y') \in S$ in the range of ϕ the equations

$$b_1 \frac{1}{1 + x + c_1 y} x = x', \quad b_2 \frac{1}{1 + c_2 x + y} y = y'$$

have the unique solution

$$x = \frac{\beta_2 - 1 + c_1}{\Delta}, \quad y = \frac{\beta_1 - 1 + c_2}{\Delta}$$

where

$$\beta_1 \doteq \frac{b_1}{x'} > 1, \quad \beta_2 \doteq \frac{b_2}{y'} > 1, \quad \Delta \doteq (\beta_1 - 1)(\beta_2 - 1) - c_1 c_2$$

(the range of ϕ is defined by the inequality $\Delta > 0$). The formulas for the pre-images x and y show the inverse ϕ^{-1} continuous.

LEMMA 1 *The map $\phi : R_+^2 \rightarrow S$ is one-one and bicontinuous.*

The points $E_0 : (0, 0)$; $E_1 : (b_1 - 1, 0)$; $E_2 : (0, b_2 - 1)$ are fixed points of the map ϕ (i.e. are equilibria of the Leslie/Gower model (1) and (2)). These are “exclusion” equilibria.

The set of points whose x -coordinate is held fixed by the map ϕ is the line $x + c_1 y = b_1 - 1$. If this line intersects \mathring{R}_+^2 (i.e. if $b_1 > 1$), we denote the resulting line segment by L_1 . Similarly, if $b_2 > 1$, the points on the line segment L_2 from the line $c_2 x + y = b_2 - 1$ lying in R_+^2 is the set of points in R_+^2 whose y -coordinate is held fixed by the map ϕ . If $b_1 > 1$ the map ϕ takes a point $(x, y) \in R_+^2$ lying above (below) L_1 to a point with smaller (larger) x -coordinate. If $b_2 > 1$ the map ϕ takes a point $(x, y) \in R_+^2$ lying above (below) L_2 to a point with smaller (larger) y -coordinate.

The only other fixed point of ϕ is

$$E_3 : \left(\frac{b_2 - 1}{c_1 c_2 - 1} \left(c_1 - \frac{b_1 - 1}{b_2 - 1} \right), \quad \frac{b_1 - 1}{c_1 c_2 - 1} \left(c_2 - \frac{b_2 - 1}{b_1 - 1} \right) \right)$$

This equilibrium lies in R_+^2 if and only if $b_1 > 1, b_2 > 1$ and L_1 and L_2 intersect in R_+^2 . This is a ‘‘coexistence’’ equilibrium.

An equilibrium is *globally asymptotically stable on R_+^2* (or $\overset{\circ}{R}_+^2$) if it is locally asymptotically stable (on R^2) and if $(x_0, y_0) \in R_+^2$ (or $\overset{\circ}{R}_+^2$) implies that (x_t, y_t) tends to the equilibrium as $t \rightarrow +\infty$.

The Jacobian of Eqs. (1) and (2) is

$$J = \begin{pmatrix} -b_1 \frac{1}{(1+x+c_1y)^2}x + b_1 \frac{1}{1+x+c_1y} & -b_1 c_1 \frac{1}{(1+x+c_1y)^2}x \\ -b_2 c_2 \frac{1}{(1+c_2x+y)^2}y & -b_2 \frac{1}{(1+c_2x+y)^2}y + b_2 \frac{1}{1+c_2x+y} \end{pmatrix}$$

The Jacobians evaluated at E_0, E_1 and E_2 are

$$J_0 = \begin{pmatrix} b_1 & 0 \\ 0 & b_2 \end{pmatrix}, \quad J_1 = \begin{pmatrix} \frac{1}{b_1} & \frac{1}{b_1}(1 - b_1)c_1 \\ 0 & \frac{b_2}{1+(b_1-1)c_2} \end{pmatrix}, \quad J_2 = \begin{pmatrix} \frac{b_1}{1+(b_2-1)c_1} & 0 \\ \frac{1}{b_2}(1 - b_2)c_2 & \frac{1}{b_2} \end{pmatrix}$$

respectively. Their eigenvalues appear along the diagonals.

LEMMA 2

- (a) If $b_1 < 1, b_2 < 1$ then E_0 is globally asymptotically stable on R_+^2 .
- (b) If $b_1 > 1, b_2 < 1$ then E_1 is globally asymptotically stable on $\overset{\circ}{R}_+^2$.
- (c) If $b_1 < 1, b_2 > 1$ then E_2 is globally asymptotically stable on $\overset{\circ}{R}_+^2$.

Proof

- (a) The eigenvalues of J_0 are less than 1 and E_0 is locally asymptotically stable. Since E_0 is the only equilibrium in R_+^2 it follows from the Liu and Elaydi’s theorem that all solutions in R_+^2 converge to E_0 . This can also be seen, more directly, from the inequalities

$$0 \leq x_{t+1} < b_1 x_t \tag{3}$$

$$0 \leq y_{t+1} < b_2 y_t \tag{4}$$

and an induction argument.

- (b) The only equilibria in R_+^2 are E_0 and E_1 . From J_0 we see that E_0 is a saddle. Since the coordinate axes are invariant, the stable manifold is the y -axis (since by Eq. (4) $y_t \rightarrow 0$). From the stable manifold and Hartman/Grobman theorems for maps [15,21], it follows that no solution in $\overset{\circ}{R}_+^2$ can approach E_0 . By Liu and Elaydi’s theorem all solutions must therefore approach E_1 . The eigenvalues of J_1 are less than 1 and E_1 is locally asymptotically stable.
- (c) This symmetric case is proved in manner analogous to case (b). □

From now on we assume $b_1 > 1, b_2 > 1$. These inequalities imply E_1 and E_2 lie on the positive x - and y -axis, respectively. We distinguish four cases depending on the orientation of the line segments L_1 and L_2 as shown in Figure 1. The inequalities satisfied by the coefficients that correspond to these cases can be easily read from the relative positions of the intercepts of L_1 and L_2 in Figure 1. In particular, the following inequalities characterize

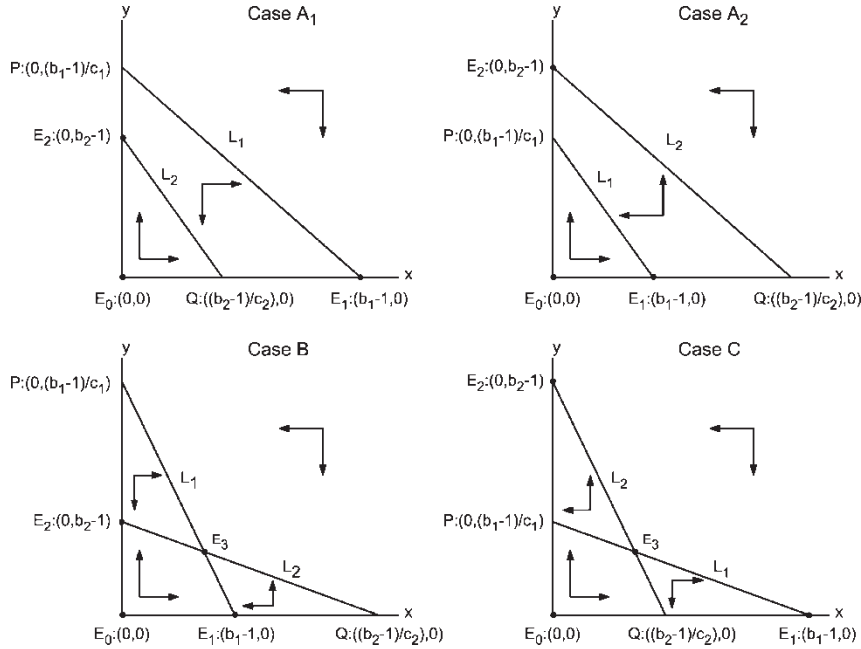


FIGURE 1 The four possible orientations of L_1 and L_2 .

Cases B and C:

$$\text{Case B : } c_1(b_2 - 1) < b_1 - 1, \quad c_2(b_1 - 1) < b_2 - 1 \tag{5}$$

$$\text{Case C : } c_1(b_2 - 1) > b_1 - 1, \quad c_2(b_1 - 1) > b_2 - 1.$$

From these inequalities we find that

$$c_1 c_2 < 1 \text{ holds in Case B} \tag{6}$$

$$c_1 c_2 > 1 \text{ holds in Case C.}$$

LEMMA 3 Assume $b_1 > 1$ and $b_2 > 1$. The equilibrium E_0 is a repellor. For $i = 1, 2$ the equilibrium E_i is locally asymptotically stable in Cases A_i and C, but is a saddle in Cases A_j ($j \neq i$) and B. In the latter two cases, the stable manifold of the saddle E_i is the positive coordinate axis on which it lies. Equilibrium E_3 is locally asymptotically stable in Case B and is a saddle in Case C.

Proof The eigenvalues of J_0 are $b_1 > 1$, $b_2 > 1$ and E_0 is therefore a repellor. The eigenvalue $1/b_1$ of J_1 is less than one. Solutions starting on the positive x -axis satisfy the Bervton/Holt equation (with $b_1 > 1$) and therefore approach E_1 . The second eigenvalue

$$\frac{b_2}{1 + c_2(b_1 - 1)}$$

is less than one in Cases A_1 and C and greater than one in Cases A_2 and B. A similar calculation shows the result for E_2 .

Finally, we consider the equilibrium E_3 , at which the Jacobian is

$$J_3 = \begin{pmatrix} \frac{c_1 c_2 b_1 - c_1 b_2 + c_1 - 1}{b_1(c_1 c_2 - 1)} & c_1 \frac{b_1 - c_1 b_2 + c_1 - 1}{b_1(c_1 c_2 - 1)} \\ c_2 \frac{-c_2 b_1 + b_2 + c_2 - 1}{b_2(c_1 c_2 - 1)} & \frac{-c_2 b_1 + c_2 c_1 b_2 + c_2 - 1}{b_2(c_1 c_2 - 1)} \end{pmatrix}.$$

This equilibrium is locally asymptotically stable if the Jury conditions

$$|\operatorname{tr} J_3| < 1 + \det J_3 < 2$$

hold, where $\det J_3$ is the determinant and $\operatorname{tr} J_3$ is the trace of J_3 [1]. If at least one of these inequalities is reversed, then the equilibrium is unstable. The inequalities are equivalent to the following three inequalities

- (a) $1 + \det J_3 < 2$
- (b) $-1 - \det J_3 < \operatorname{tr} J_3$
- (c) $\operatorname{tr} J_3 < 1 + \det J_3$.

A calculation shows

$$\det J_3 = \frac{c_2(c_1 - 1)(b_1 - 1) + c_1(c_2 - 1)(b_2 - 1) + c_1 c_2 - 1}{b_1 b_2 (c_1 c_2 - 1)}$$

$$\operatorname{tr} J_3 = \frac{2b_2 b_1 c_1 c_2 - b_2 + c_1 b_2 - c_1 b_2^2 - b_1 + c_2 b_1 - c_2 b_1^2}{b_1 b_2 (c_1 c_2 - 1)}.$$

Using these formulas, we find that inequality (a) is equivalent to

$$(b_1 - 1)(b_2 - 1) + \frac{c_1(b_2 - 1) - (b_1 - 1)}{c_1 c_2 - 1} + \frac{c_2(b_1 - 1) - (b_2 - 1)}{c_1 c_2 - 1} > 0.$$

By Eqs. (5) and (6) this inequality holds. Inequality (b) is equivalent to

$$(b_1 + 1)(b_2 + 1) + c_2(b_1 + 1) \frac{c_1(b_2 - 1) - (b_1 - 1)}{c_1 c_2 - 1} + c_1(b_2 + 1) \frac{c_2(b_1 - 1) - (b_2 - 1)}{c_1 c_2 - 1} > 0$$

which Eqs. (5) and (6) show also holds true. Finally, we consider inequality (c), which it turns out is equivalent to

$$\frac{(c_1(b_2 - 1) - (b_1 - 1))(c_2(b_1 - 1) - (b_2 - 1))}{c_1 c_2 - 1} < 0.$$

From Eqs. (5) and (6), we see that this inequality holds in Case B and, as a result, E_3 is locally asymptotically stable. In Case C, however, the reverse inequality holds and E_3 is unstable.

To see, in the latter case, that E_3 is in fact a saddle we note that the characteristic quadratic polynomial of J_3 , namely,

$$p(\lambda) = \lambda^2 - (\operatorname{tr} J_3)\lambda + \det J_3$$

satisfies $p(1) = 1 - \text{tr}J_3 + \det J_3 < 0$ (because the inequality in (c) is reversed in Case C), $p(-1) = 1 + \text{tr}J_3 + \det J_3 > 0$ (because (b) holds), and $p(+\infty) = +\infty$. Thus, $p(\lambda)$ has a positive root $\lambda > 1$ and a root between -1 and $+1$. \square

THEOREM 4 *Consider the Leslie/Gower competition model (1) and (2) with $b_i > 1$. Each component x_t and y_t of a solution in \mathring{R}_+^2 is eventually monotonic.*

- (a) *In Case A_i, the equilibrium E_i is globally asymptotically stable on \mathring{R}_+^2 .*
- (b) *In Case B, the equilibrium E_3 is globally asymptotically stable on \mathring{R}_+^2 .*
- (c) *In Case C, for solution in \mathring{R}_+^2 tends to one of the locally asymptotically stable equilibria E_1 or E_2 or to the saddle equilibrium E_3 as $t \rightarrow +\infty$.*

Proof Every solution in \mathring{R}_+^2 is eventually monotonic and converges to one of the four equilibria E_i by Liu and Elyaydi’s theorem.

- (a) The two Cases A_1 and A_2 are symmetric and we consider Case A_1 only. Observe that the (closed) triangular region E_0E_1P is forward invariant under the map ϕ . This follows from two facts: ϕ is one-to-one and bicontinuous (Lemma 1) and the boundary of E_0E_1P maps into E_0E_1P (see Fig. 1). Thus, if a solution starts in the triangle E_0E_1P is remains there and as a result the component x_t is increasing. It follows that the solution approaches E_1 . If, on the other hand, $(x_0, y_0) \in \mathring{R}_+^2$ lies outside the triangle E_0E_1P there are two options: either the solution sequence (x_t, y_t) enters the triangle in a finite number of steps, in which case it will remain there and converge to E_1 (as we just proved), or it remains outside the triangle for all t . In the latter case, the solution can only converge to E_1 . In summary, $(x_0, y_0) \in \mathring{R}_+^2$ implies (x_t, y_t) tends E_1 as $t \rightarrow +\infty$. This, together with Lemma 3, shows E_1 is globally asymptotically stable on \mathring{R}_+^2 .
- (b) By Lemma 3, E_3 is locally asymptotically stable. The discrete stable manifold and Hartman/Grobman theorems, together with Lemma 3, imply that no orbit in \mathring{R}_+^2 can approach E_0, E_1 or E_2 . It follows from Liu and Elyaydi’s theorem that all orbits in \mathring{R}_+^2 approach E_3 .
- (c) By Lemma 3, E_0 is a repellor and cannot be approached by a solution in \mathring{R}_+^2 . \square

For case (c) in Theorem 4 we do not have a complete characterization of the basins of attraction for each equilibrium. From the stable manifold theorem for maps [15,21] we know the local stable manifold of E_3 is one dimensional (since by Lemma 2 the equilibrium E_3 is a hyperbolic saddle in Case C), but we do not know if this is globally true in \mathring{R}_+^2 . We can show that the basin of attraction of E_1 contains the interior of the closed triangle QE_1E_3 . To see this notice that ϕ maps the boundary of the triangle into the triangle: $\phi : \partial(QE_1E_3) \rightarrow QE_1E_3$ (see Fig. 1). Since ϕ is one–one and bicontinuous, it follows that $\phi : QE_1E_3 \rightarrow QE_1E_3$ (i.e. QE_1E_3 is forward invariant). Solutions starting in (or eventually entering) the interior of QE_1E_3 must accordingly approach the equilibrium E_1 . Similarly, one can show that the basin of attraction of E_2 contains the interior of the triangle PE_2E_3 .

The four dynamic cases in Theorem 4 (and Fig. 1) are the same as those in the Lotka/Volterra model and have the same ecological interpretation. Coexistence (Case B) occurs if interspecific competition is weak in the sense that the coefficients c_i are small:

$$c_1 < \frac{b_1 - 1}{b_2 - 1}, \quad c_2 < \frac{b_2 - 1}{b_1 - 1}.$$

If interspecific competition is too large (one or both inequalities are reversed), then competitive exclusion occurs. This is the theoretical foundation for the classical competitive exclusion principle. It is because of this principle that the anomolous case observed in some of Park's experiments were puzzling. In the next section, we will study a competition model which does not support this exclusion principle—a model which in fact predicts (non-equilibrium) coexistence when the competition coefficients are *increased*.

A JUVENILE/ADULT RICKER MODEL

Since the Leslie/Gower competition model (1) and (2) has only the Lotka/Volterra dynamics described in Theorem 4, this model offers no explanation of the multiple attractor case (with initial condition dependent coexistence or exclusion) observed by Park. A discrete competition model that does provide an explanation is the so-called LPA model [10–12]. This six dimensional model is based on three life cycle stages for each species and was derived explicitly to study the dynamics of flour beetle species. See Ref. [14] for an account of the LPA competition model and some of its non-Lotka/Volterra dynamics that contradict the classical competitive exclusion principle.

A mathematical exploration of competition models that possess multiple attractor cases with initial condition dependent coexistence or exclusion might start with the Leslie/Gower model and try to determine what kinds of structural changes in the model will result in non-Lotka/Volterra dynamics and contradictions to the competitive exclusion principle. For example, if exponential non-linearities replace the rational function non-linearities of the Leslie/Gower model, one obtains the Ricker competition model

$$\begin{aligned}x_{t+1} &= b_1 x_t \exp(-c_{11} x_t - c_{12} y_t) \\ y_{t+1} &= b_2 y_t \exp(-c_{21} x_t - c_{22} y_t)\end{aligned}$$

(exponential non-linearities also appear in the LPA model). Numerical investigations of this model have uncovered certain kinds of non-Lotka/Volterra dynamics [10], but not a case of multiple attractors with both coexistence and exclusion. Whether or not such multiple attractor cases can occur in this system remains an interesting open question.

From a mathematical point of view life cycle stages (such as appear in the LPA model) introduce time delays. A modification of the Ricker competition model, in which individuals from one of the two species are characterized by their reproductive maturity, is described by the difference equations

$$\begin{aligned}J_{t+1} &= b_1 A_t \exp(-c_{11} A_t - c_{12} y_t) \\ A_{t+1} &= (1 - \mu) J_t \\ y_{t+1} &= b_2 y_t \exp(-c_{21} J_t - c_{22} y_t).\end{aligned}\tag{7}$$

Here J_t and A_t are the numbers of juveniles and adults at time t of the species x . Species y in this model remains unstructured. The parameter μ ($0 \leq \mu < 1$) is the juvenile mortality rate.

In this paper, we will not attempt a thorough analysis of the juvenile/adult Ricker competition model (7). We will only show that under certain conditions the model possesses three attractors, two exclusion (equilibrium) attractors and one (non-equilibrium) coexistence attractor.

The exclusion equilibria for Eq. (7) are

$$E_0 : (J, A, y) = (0, 0, 0)$$

$$E_1 : (J, A, y) = \left(\frac{\ln n}{c_{11}(1 - \mu)}, \frac{\ln n}{c_{11}}, 0 \right)$$

$$E_2 : (J, A, y) = \left(0, 0, \frac{\ln b_2}{c_{22}} \right).$$

Here we have defined $n \triangleq b_1(1 - \mu)$ [9]. We assume $n > 1, b_2 > 1$ so that these equilibria are non-negative. The Jacobian at E_0

$$\begin{pmatrix} 0 & b_1 & 0 \\ -\mu + 1 & 0 & 0 \\ 0 & 0 & b_2 \end{pmatrix}$$

has eigenvalues $\lambda = b_2$ and $\pm\sqrt{n}$. The Jacobian at E_1

$$\begin{pmatrix} 0 & \frac{1-\ln n}{n}b_1 & -\frac{b_1c_{12}\ln n}{c_{11}n} \\ 1 - \mu & 0 & 0 \\ 0 & 0 & b_2 \exp\left(-\frac{c_{21}\ln n}{c_{11}(1-\mu)}\right) \end{pmatrix}$$

has eigenvalues $\lambda = \pm\sqrt{1 - \ln n}$ and $b_2 \exp(-c_{21}\ln n/c_{11}(1 - \mu))$. The Jacobian at E_2

$$\begin{pmatrix} 0 & b_1 e^{-\frac{c_{12}}{c_{22}}\ln b_2} & 0 \\ 1 - \mu & 0 & 0 \\ -\frac{c_{21}}{c_{22}}\ln b_2 & 0 & 1 - \ln b_2 \end{pmatrix}$$

has eigenvalues $\lambda = \pm\sqrt{n}$ and $1 - \ln b_2$.

THEOREM 5 Assume $n = b_1(1 - \mu) > 1, b_2 > 1$ in the juvenile/adult Ricker competition model (7).

- (a) E_0 is a repellor.
- (b) E_1 is locally asymptotically stable if

$$1 < n < e^2, \quad c_{11}(1 - \mu) \frac{\ln b_2}{\ln n} < c_{21}.$$

- (c) E_2 is locally asymptotically stable if

$$1 < b_2 < e^2, \quad c_{22} \frac{\ln n}{\ln b_2} < c_{12}.$$

The ecological interpretation of the parameter inequalities in Theorem 5(b) and (c) is that interspecific competition is sufficiently strong (as measured by c_{12} and c_{21}), relative to intraspecific competition (measured by c_{11} and c_{22}). This theorem suggests the Lotka/Volterra or Leslie/Gower “saddle” case of competitive exclusion (Case C in Fig. 1). However, it is possible that all the inequalities in Theorem 5 hold and there also exists

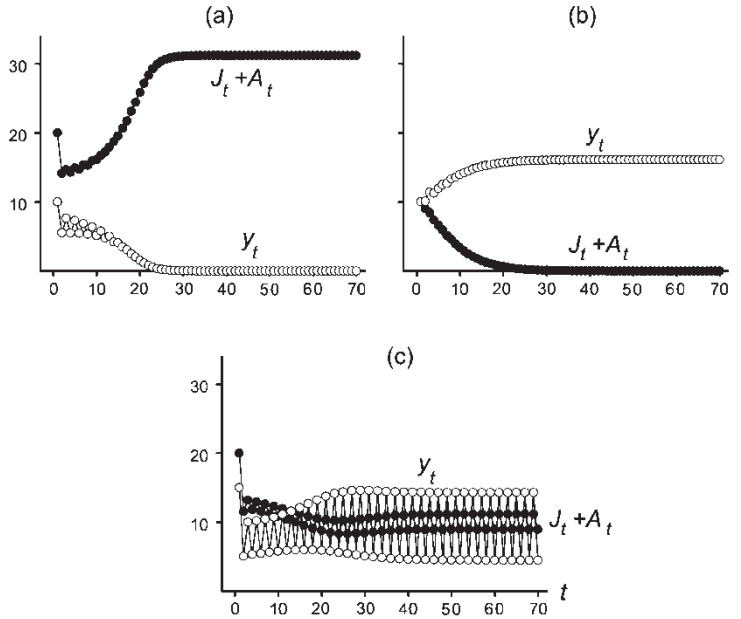


FIGURE 2 Three different initial conditions lead to solutions of the juvenile/adult Ricker competition model (7) that approach three different attractors. (a) The initial condition $(J_0, A_0, y_0) = (10, 10, 10)$ results in an orbit that approaches an equilibrium in which $y = 0$, i.e. this initial condition leads to the extinction of species y . (b) The initial condition $(J_0, A_0, y_0) = (5, 5, 10)$ results in an orbit that approaches an equilibrium in which $J = A = 0$, i.e. this initial condition leads to the extinction of species x . (c) The initial condition $(J_0, A_0, y_0) = (10, 10, 15)$ results in an orbit that approaches a positive two-cycle, i.e. the initial condition leads to the (non-equilibrium) coexistence of both species. The coefficients in these examples are $b_1 = b_2 = 5$, $c_{11} = c_{22} = 0.1$, $c_{12} = 0.11$, $c_{21} = 0.12$, and $\mu = 0.2$.

a coexistence attractor. Figure 2 shows an example. In that figure one initial condition approaches a coexistence two-cycle, while other initial conditions lead to the extinction equilibria E_1 and E_2 .

It is possible to prove the existence of coexistence two-cycles of the type observed in Figure 2. Two-cycles are fixed points of the composite map defined by the model equations (7)

$$\begin{aligned}
 b_1(1 - \mu)J \exp(-c_{11}(1 - \mu)J - b_2c_{12}ye^{-c_{21}J - c_{22}y}) &= J \\
 b_1(1 - \mu)Ae^{-c_{11}A - c_{12}y} &= A \\
 b_2^2ye^{-c_{21}J - c_{22}y} \exp(-b_1c_{21}Ae^{-c_{11}A - c_{12}y} - b_2c_{22}ye^{-c_{21}J - c_{22}y}) &= y.
 \end{aligned}
 \tag{8}$$

Although it is not shown in Fig. 2, the coexistence two-cycle in that example is synchronous, i.e. the two points of the cycle are of the form

$$(0, A, y_1), \quad (J, 0, y_2)
 \tag{9}$$

with $J > 0, A > 0$, and $y_i > 0$. ‘‘Synchronous’’ means that the juvenile and adult populations never appear together at the same point in time. The two-cycle equations (8) with $J = 0$ reduce to the two equations

$$\begin{aligned}
 b_1(1 - \mu)e^{-c_{11}A - c_{12}y} &= 1 \\
 b_2^2e^{-c_{21}J - c_{22}y} \exp(-b_1c_{21}Ae^{-c_{11}A - c_{12}y} - b_2c_{22}ye^{-c_{21}J - c_{22}y}) &= 1
 \end{aligned}$$

for A and y . Using the first equation in the second we can simplify the second equation

$$b_1(1 - \mu)e^{-c_{11}A - c_{12}y} = 1$$

$$b_2^2 \exp\left(-c_{22}y - c_{21} \frac{1}{1 - \mu}A - b_2c_{22}ye^{-c_{22}y}\right) = 1.$$

Solving the first equation for

$$A = \frac{1}{c_{11}}(\ln n - c_{12}y) \tag{10}$$

substituting this result into the second equation and simplifying, we arrive at the single equation

$$b_2c_{22}ye^{-c_{22}y} = \left(\frac{c_{12}c_{21}}{(1 - \mu)c_{11}} - c_{22}\right)y + \left(2 \ln b_2 - \frac{c_{21}}{(1 - \mu)c_{11}} \ln b_1(1 - \mu)\right) \tag{11}$$

for y . A solution $y = y_1 > 0$, together with Eq. (10), yields the first point in a two-cycle (9). (If $A > 0$ then this point is not an equilibrium.) The Eq. (11) can be analyzed geometrically by investigating the graphs of both sides of the equation for intersection points $y > 0$. The left hand side is a positive, one humped graph passing through $y = 0$ and having $y = 0$ as an asymptote. The right hand side is a straight line whose slope is positive under the assumptions in Theorem 5(b) and (c). If the y -intercept of the straight line is positive, then either there are two intersection points of these graphs, no intersection point at all, or a tangency case of one intersection point. As parameters change and we pass from one to the other case, a bifurcation occurs at the point of tangency. (We speculate that this is a saddle node bifurcation with another two-cycle which, because it is not a synchronous cycle, is not found by the equations above.) See Figure 3 for an illustration. Note that the coexistence two-cycle is created in this example by *increasing* the interspecific competition coefficient c_{21} !

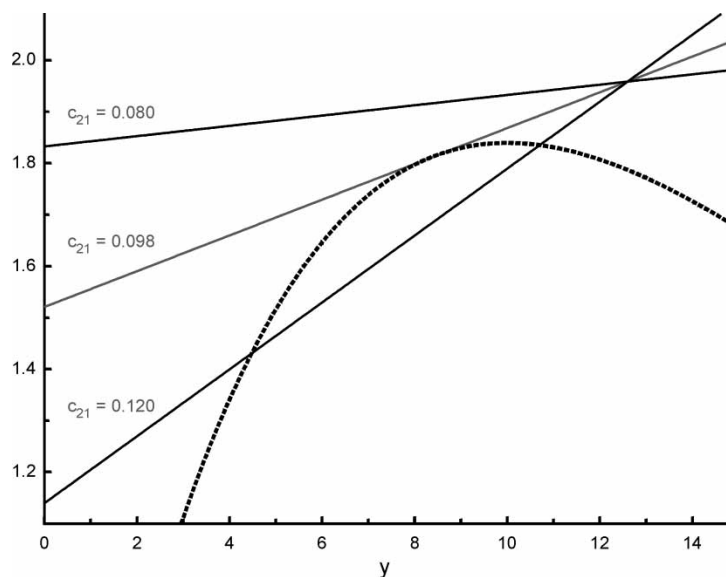


FIGURE 3 Roots $y > 0$ of Eq. (9) determine synchronous two-cycles for the juvenile/adult Ricker competition model (7). The dashed line graph is that of the left hand side of this equation for the parameter values in Fig. 2. The straight line graphs are the right hand side of the equation for three selected values of the interspecific competition coefficient c_{21} . For the smaller value of c_{21} there is no intersection and there exists no synchronous two-cycle. For the larger value of c_{21} , two intersection points exist and give rise to a synchronous two-cycle.

To establish the triple attractor case of interest (and observed in Fig. 2) we need to prove the stability of the two-cycle under the conditions of Theorem 5(b) and (c). The two-cycle is locally asymptotically stable if the eigenvalues of the Jacobian of the composite map are less than one in magnitude. We can calculate this Jacobian by multiplying the Jacobians of the (7) evaluated at the two points of the two-cycle. In general, this calculation is intractable, but we can carry it out for the example in Figure 2. For the parameter values in that example, Eq. (11) has the two solutions $y_1 = 4.4758$ and $y_2 = 14.304$ which produce the two-cycle points (see Eq. (9))

$$(0, 8.9396, 4.4758), \quad (11.1174, 0, 14.304).$$

The Jacobians of Eq. (7) at these two points, when multiplied, yield the matrix

$$\begin{pmatrix} 0.76624 & 0 & 0.16554 \\ 0 & 0.82932 & 0 \\ -0.94822 & -1.7794 & -0.23776 \end{pmatrix}$$

whose eigenvalues $\lambda = -4.4039 \times 10^{-2}$, 0.57252 , and 0.82932 are less than one in magnitude. The two-cycle is therefore locally asymptotically stable. Since the inequalities in Theorem 5(b) and (c) are satisfied by the parameters in this example the two exclusion equilibria

$$E_1 : (J, A, y) = (20.118, 16.094, 0)$$

$$E_2 : (J, A, y) = (0, 0, 16.094)$$

are also locally asymptotically stable.

The juvenile/adult Ricker competition model shows that strong non-linearities and a time delay can produce a multiple attractor, coexistence/exclusion, scenario. According to our analysis above this scenario arises from a bifurcation that gives rise to a two-cycle coexistence state as interspecific competition is *increased*, which from the point of view of classical competition theory is unexpected. This same bifurcation scenario occurs in the LPA model [14]. Thus, we have two examples of competition models that provide dynamics which contradict classical competition theory in significant ways. An interesting open mathematical problem is to determine the types of competition models that possess these kinds of multiple attractors.

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