JOURNAL OF PURE AND APPLIED MICROBIOLOGY, April 2013. Vol. **7**(Spl. Edn.), p. 215-219

Dynamics of Juvenile/Adult Ricker Competition Models

Wei Xiong[1], Yonghui Cao[1,2] and He Jiang[3]

[1]School of Management, Zhejiang University, China.
[2] School of Economics & Management, Henan Institute of Science and Technology, China.
[3]Department of Mathematics, Henan Institute of Science and Technology, China.

(Received: 03 March 2013; accepted: 14 April 2013)

The specie has the age structure, including the juvenile stage and adult stage, the other specie remains unstructured. This paper studies the stability and permanence of the Juvenile/Adult Ricker competition model. Using Lyapunov exponent we analyze the dynamic behaviors of this model, and obtain the existence of the multiple mixed-type attractor which explains the multiple mixed-type attractor phenomenon that found in the lab by Park.

Key words: Difference equation; Competition model; Multiple mixed-type attractor.

Competitive exclusion principle is a fundamental tenet in theoretical ecology. 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 model. The Lotka/Volterra model has four dynamic scenarios, all of which involve only equilibria as possible asymptotic states. A coexistence case occurs if the competition between the species is weak. If, however, the inter-species competition is sufficiently strong, then competitive exclusion principle occurs. 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, has an unstable coexistence equililbrium.

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 was conducted by Park and Mertz using two species of flour beetles (of the genus Tribolium)[1-4]. It is interesting that although Park's experiments was considered a validation of the competitive exclusion principle, there were some unusual aspects with regard to classic competition theory, including non-equilibrium dynamics, coexistence under increased intensity of inter-specific competition, and the occurrence of multiple mixed-type attractors. By multiple mixed-type attractors we mean a scenario that include at least one coexistence attractor and at least one exclusion attractor. An coexistence attractor is one in which both species are present. An exclusion attractor is one in which at least one species is absent and at least one species is present. Park observed the coexistence case in an experimental treatment that also included cases of competitive exclusion, that is to say, he observed a case of what we have termed to be multiple mixed-type attractor.

Which type competitive model contradicted the competitive exclusion principle and explained the observed case of multiple mixed-

* To whom all correspondence should be addressed.
E-mail: caoyonghui2000@126.com;
lurky2000@126.com

type attractor[5]. Give us an example Juvenile/Adult Ricker competition models except LPA model which contradicted the competitive exclusion principle[5]. Show that under certain conditions the model possesses three attractors, two exclusion attractors and one coexistence attractor. In this paper we assume Species y is the stage-structured Richer equation which extends the conclusion in [5].

RESULTS

$$\begin{cases} J_{t+1}=b_1 A_t e^{-c_{11}A_t-c_{12}y_t} \\ A_{t+1}=(1-\mu)J_t \\ y_{t+1}=b_2 y_t e^{-c_{21}A_t-c_{22}y_t}+sy_t \end{cases} \quad \text{... (1)}$$

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 $\mu(0<\mu<1)$ is juvenile mortality rate. The $b_i(b_i>0,i=1,2)$ are the inherent birth rates. $s(0<s<1)$ is the survival rates and $c_{ij}(c_{ij}>0,i=1,2;j=1,2)$ is the density- dependent effects on newborn recruitment. the extinction equilibria for (1) is $E_0=(0,0,0)$;
the exclusion equilibrium for (1) are

$$E_1=\left(\frac{\ln n}{c_{11}(1-\mu)},\frac{\ln n}{c_{11}},0\right),\ E_2=\left(0,0,\frac{\ln\frac{b_2}{1-s}}{c_{22}}\right);$$

the coexistence equilibria for (1) is

$$E_3=\left(\frac{c_{12}\ln\frac{b_2}{1-s}-c_{22}\ln n}{c_{12}c_{21}-c_{11}c_{22}(1-\mu)},\frac{c_{12}\ln\frac{b_2}{1-s}-c_{22}\ln n}{c_{12}c_{21}-c_{11}c_{22}(1-\mu)}(1-\mu),\frac{c_{21}\ln n-c_{11}(1-\mu)\ln\frac{b_2}{1-s}}{c_{12}c_{21}-c_{11}c_{22}(1-\mu)}\right)=(J^*,A^*,y^*)$$

Here we have deûned $n=b_1(1-\mu)$, we assume $n>1,\ b_2+s>1,$ so that these equilibrium are non-negative.

Theorem 2.1

Assume $n>1, b_2+s>1,$ the extinction equilibria $E_0=(0,0,0)$ is a repellor.

Proof. The Jacobian at E_0 is $\begin{pmatrix} 0 & b_1 & 0 \\ 1-\mu & 0 & 0 \\ 0 & 0 & b_2+s \end{pmatrix}$

has eigevalues $|\lambda_1|=b_2+s>1,\ \lambda_2^2=\lambda_3^2=b_1(1-\mu)>1$,so the extinction equilibria $E_0=(0,0,0)$ is a repellor.

Theorem 2.2

Assume $e>n>1, b_2+s>1,$

(1) if $\frac{c_{11}(1-\mu)\ln\frac{b_2}{1-s}}{\ln n}<c_{21}$, the exclusion equilibria E_1 is locally asymptotically stable;

(2) if $\frac{c_{11}(1-\mu)\ln\frac{b_2}{1-s}}{\ln n}=c_{21}$, the exclusion equilibria E_1 is locally asymptotically closed orbit;

(3) if $\frac{c_{11}(1-\mu)\ln\frac{b_2}{1-s}}{\ln n}>c_{21}$,the exclusion equilibria E_1 is chaotic.

Proof. The Jacobian at E_1 is $\begin{pmatrix} 0 & \frac{(1-\ln n)b_1}{n} & \frac{-b_1c_{12}\ln n}{nc_{11}} \\ 1-\mu & 0 & 0 \\ 0 & 0 & b_2e^{-\frac{c_{21}\ln n}{c_{11}(1-\mu)}}+s \end{pmatrix}$

has eigenvalues $|\lambda_1|=b_2e^{-\frac{c_{21}\ln n}{c_{11}(1-\mu)}}+s$, $\lambda_2^2=\lambda_3^2=1-\ln n$.

(1) if $e>n>1, b_2+s>1$, $\frac{c_{11}(1-\mu)\ln\frac{b_2}{1-s}}{\ln n}<c_{21}$, the eigenvalues $|\lambda_1|<1,|\lambda_{2,3}|<1$, so we know that $L(p,x^1;F)=\ln|\lambda_1|<0$; $L(p,x^2;F)=\ln|\lambda_2|<0$; $L(p,y^3;F)=\ln|\lambda_3|<0$
By the relationship of Lyapunov exponent and dynamical properties, we could obtain the exclusion equilibria E_1 is locally asymptotically stable.

We could proof (2), (3) and theorems 2.3 in the same way.

Theorem 2.3

(1)Assume $n>1,\ b_2+s>1,\ 0<b_2<(1-s)e^{\frac{2}{1-s}}$,

(i) if $\frac{c_{22}\ln n}{\ln\frac{b_2}{1-s}}<c_{12}$, the exclusion equilibria E_2 is locally asymptotically stable;

(ii) if $\frac{c_{22}\ln n}{\ln\frac{b_2}{1-s}}=c_{12}$, the exclusion equilibria is locally asymptotically stable two-dimensional torus(quasi-period vibration);
(iii) if ,the exclusion equilibria is chaotic.
(2)Assume ,
(i) if , the exclusion equilibria is locally asymptotically closed orbit (period vibration);
(ii) if ,the exclusion equilibria is chaotic.
(3) Assume , the exclusion equilibria is chaotic.

Theorem 2.4

If the interspecific competition is suûciently strong the coexistence equilibria is unstable (chaotic).

Proof. The Jacobian at is

$$\begin{pmatrix} 0 & \frac{1-c_{11}A^*}{1-\mu} & -c_{12}J^* \\ 1-\mu & 0 & 0 \\ (s-1)c_{21}y^* & 0 & (1-c_{22}y^*)(1-s)+s \end{pmatrix}$$

The characteristic equation of the coexistence equilibria is

$$f(\lambda)=[(1-c_{22}y^*)(1-s)+s]\lambda^2-[(1-c_{11}A^*)+c_{12}c_{21}(1-s)y^*J^*]\lambda+(1-c_{11}A^*)[(1-c_{22}y^*)(1-s)+s]$$

$$f(1)=(1-s)[c_{11}c_{22}(1-\mu)-c_{12}c_{21}]y^*J^*$$

we know that $c_{12}c_{21}>c_{11}c_{22}(1-\mu)$, so $f(1)<0$.

Because $\lim_{\lambda\to+\infty}f(\lambda)>0$, the equation $f(\lambda)=0$ at least has one root which is bigger than 1. The coexistence equilibria is unstable (chaotic). In order to investigate the possible occurrence of mixed-type non-equilibrium attractors in the model (1) under symmetrically high inter-speciûc competition (as has been observed in more complicated models that include juvenile life-cycle stages). We can assume without loss in generality (by scaling the unites of x and y that $c_{11}=c_{22}=1$, to study this investigation by means of a single parameter problem, we can introduce the notation and $c=c_{12}, r=\frac{c_{21}}{c_{12}}$ re-write the competition model (1) as

$$\begin{cases} J_{t+1}=b_1(1-\mu)J_{t-1}e^{-(1-\mu)J_{t-1}-cy_t} \\ y_{t+1}=b_2y_te^{-rx_t-y_t}+sy_t \end{cases} \quad ...(2)$$

In absence of species $x(J_t=0)$, the dynamics of species are governed by the Ricker model equation

$$y_{t+1}=b_2y_te^{-y_t}+sy_t \quad ...(3)$$

we can get the equilibrium : $y_0=\ln\frac{b_2}{1-s}$, $b_2^{cr}\overset{\Delta}{=}(1-s)e^{\frac{2}{1-s}}$.

Theorem 2.5

If $b_2<b_2^{cr}$, the equilibrium of the model (3) is stable.

Proof: we know that $|f'_{y}(y_0)|=|b_2e^{-y_0}-b_2y_0e^{-y_0}+s|=\left|(1-s)(1-\ln\frac{b_2}{1-s})+s\right|<1$, so the equilibrium $y_0=\ln\frac{b_2}{1-s}$ of the model (3)is stable.

Theorem 2.6

If , $b_2\ge b_2^{cr}$ (2) has stable 2-cycle

$$y_0^*\to y_1^*\to y_0^*\to y_1^*\to\cdots,\ (0<y_1^*<y_0^*) \quad ...(4)$$

the two points y_1^*, y_0^* satisfy the equation

$$\begin{cases} y_0^*=b_2y_1^*e^{-y_1^*}+sy_1^* \\ y_1^*=b_2y_0^*e^{-y_0^*}+sy_0^* \end{cases}$$

Proof: Assume $f(y)=b_2ye^{-y}+sy$, the only equilibrium is $y_0=\ln\frac{b_2}{1-s}$,

$$f^2(y)=b_2(b_2ye^{-y}+sy)e^{-(b_2ye^{-y}+sy)}+s(b_2ye^{-y}+sy)$$
$$=y(b_2e^{-y}+s)(b_2e^{-b_2ye^{-y}-sy}+s)$$

So the equation $0=f^2(y)-y=y(b_2e^{-y}+s)(b_2e^{-b_2ye^{-y}-sy}+s)-y$ has the roots $y_0=\ln\frac{b_2}{1-s}$, $y_2=y_0^*$, $y_3=y_1^*$, and y_0^*, y_1^* satisfy the equation $\begin{cases} y_0^*=b_2y_1^*e^{-y_1^*}+sy_1^* \\ y_1^*=b_2y_0^*e^{-y_0^*}+sy_0^* \end{cases}$

Because $y=\ln\frac{b_2}{1-s}$ is the equilibrium of $f(y)=y$, the new equilibria of $f^2(y)=y$ are

$$y_2=y_0^*, y_3=y_1^*, y_0^*=f(y_1^*), y_1^*=f(y_0^*)$$

$$D(f^2)(y_0^*)=Df(y_1^*)Df(y_0^*)=\prod_{i=0}^{i=1}[(1-y_i^*)b_2e^{-y_i^*}+s]<1$$

$$D(f^2)(y_1^*)=Df(y_0^*)Df(y_1^*)=\prod_{i=0}^{i=1}[(1-y_i^*)b_2e^{-y_i^*}+s]<1$$

so, (2) has stable 2-cycle $y_0^*\to y_1^*\to y_0^*\to y_1^*\to\cdots$.

The difference system exits two stable equilibria after twice iteration which means the system
xists stable 2-cycle.

The 2-cycle (4) yields an exclusion 2-cycle.

$$(0,y_0^*)\to(0,y_1^*)\to(0,y_0^*)\to(0,y_1^*)\to\cdots \quad ...(5)$$

of the model (2). This 2-cycle is stable on the (invariant) y-axis under the assumption .
Next we will study the stability of this exclusion 2-cycle in the x,y-plane and determine how it depends on the competition intensity .

Theorem 2.7

Assume $b_2\ge b_2^{cr}$, $b_1(1-\mu)>1$. Let denote the unique positive root of the equation

$\prod_{i=0}^{1}[b_i(1-\mu)e^{-cy_i^*}+s]=1$,

(i) if $c > c^*$, the exclusion 2-cycle (5) of the competition model (2) is stable;

(ii) if $c < c^*$, the exclusion 2-cycle (5) of the competition model (2) is unstable.

Proof

The Jacobian at $(0,y_1^*)$ is $\begin{pmatrix} b_1(1-\mu)e^{-cy_1^*} & 0 \\ -b_2 c y_1^* e^{-y_1^*} & (1-y_0^*)b_2 e^{-y_1^*}+s \end{pmatrix}$

The Jacobian at $(0,y_1^*)$ is $\begin{pmatrix} b_1(1-\mu)e^{-cy_0^*} & 0 \\ -b_2 c y_1^* e^{-y_0^*} & (1-y_1^*)b_2 e^{-y_0^*}+s \end{pmatrix}$

the eigenvalues of the matrix $J(0,y_0^*)\ J(0,y_1^*)$, are

$$\lambda_1=\prod_{i=0}^{1}[b_i(1-\mu)e^{-cy_i^*}]>0,\ \lambda_2=\lambda^*=\prod_{i=0}^{1}[b_i(1-y_i^*)e^{-y_i^*}+s]$$

Under the assumption $b_2 \geq b_2^{cr}$, $0<\lambda_2<1$

As a function of , the first eigenvalue and satisfies it follows that there exits a unique $c^*>0$, such that $\lambda(c^*)=1$.

So that if $c>c^*, \lambda_1<1$, the exclusion 2-cycle (5) of the competition model (2) is stable; if $c>c^*$, $\lambda_1>1$, the exclusion 2-cycle (5) of the competition model (2) is unstable.

Assume $0<s<1, b_2 \geq b_2^{cr}$. The bifurcating stable 2-cycle (4)of the Ricker equation $y_{t+1}=b_2 y_t e^{-y_t}+sy_t\quad y_0>0$ have for $\varepsilon \neq 0$, the representations

$$y_0^*=\frac{2}{1-s}+\varepsilon+\frac{1-3s+6s^2}{6(1-s)}\varepsilon^2+o(\varepsilon^3)\qquad y_1^*=\frac{2}{1-s}-\varepsilon+\frac{1+3s}{6(1-s)}\varepsilon^2+o(\varepsilon^3)$$

The loss of stability of the exclusion 2-cycle (5) describled in Theorem 2.7 suggest the occur- rence of a bifurcation of planar 2-cycle from the exclusion 2-cycle (5). 2-cycles of the map deûned by (2) correspond to fixed points of the composite map. The point corresponding to the exclusion 2-cycle (5) is a fixed point of the composite for all values of . On the other hand, a positive fixed point $(x,y)\in R_+^2$ of the composite corresponds to a coexistence 2-cycle.

Positive fixed points of the composite satisfy the equations

$f(x,y,c)=0; \qquad g(x,y,c)=0$

Where

$f(x,y,c)=-1+b_1^2(1-\mu)^2\exp(-(1-\mu)x(1+b_1(1-\mu)e^{[illegible]})-cy(1+b_2 e^{[illegible]}+s))$

$g(x,y,c)=-1+(b_2 e^{[illegible]}+s)(b_2\exp(-xcb_1(1-\mu)xe^{[illegible]}-b_2 ye^{[illegible]}-sy)+s)$

Note that by the way that c^* is defined, the point $(x,y)=(0,y_0^*)$ still satisfies these equations when .

$f(0,y_0^*,c^*)=0;\quad g(0,y_0^*,c^*)=0$

The Implicit Function Theorem implies the existence of a solution branch $(x,y,c)=(x,y(x),c(x))$ of the equation

$$\begin{cases} f(x,y,c)=0 \\ g(x,y,c)=0 \end{cases} \qquad ...(6)$$

that passes through this point, i.e. a branch such that $(0,y(0),c(0))=(0,y_0^*,c_0^*)$

Theorem 2.8

Assume $0<s<1, b_1(1-\mu)>1$. If $b_2 \geq b_2^{cr}$, then a branch of coexistence 2-cycle bifurcates from the exclusion 2-cycle (5) at $c=c^*$.

Proof. Define ,and re-write the composite equation (6) as

$$\begin{cases} p(x,z,\omega)=-1+b_1^2(1-\mu)^2 e^{p_1(x,z,\omega)}=0 \\ q(x,z,\omega)=-1+(b_2 e^{[illegible]}+s)(b_2 e^{q_1(x,z,\omega)}+s)=0 \end{cases} \qquad ...(7)$$

where

$p_1(x,z,\omega)=-(1-\mu)x(1+b_1(1-\mu)e^{[illegible]})-(c^*+\omega)(y_0^*+z)(1+b_2 e^{[illegible]}+s))$

$q_1(x,z,\omega)=-x(c^*+\omega)b_1(1-\mu)xe^{[illegible]}-(y_0^*+z)(1+b_2 e^{[illegible]}+s)$

by the Implicit Function Theorem $\delta \square p_z' q_\omega' - p_\omega' q_z' |_{(0,0,0)} \neq 0$, if , there exists a (unique, analytic) solution $z=z(x), \omega=\omega(x)$ of (7) for on an open interval containing $x=0$, that satisfies $z(0)=\omega(0)=0$.

We can get $q_\omega'(0,0,0)=0$, $p_\omega'(0,0,0)=-y_0^*(1+b_2 e^{-y_0^*}+s)b_1^2(1-\mu)^2 e^{p_1(0,0,0)}<0$, $q_z'(0,0,0)>0$

Since $\delta \neq 0$, the Implicit Function Theorem implies there exists a (unique, analytic) solution pair $z=z(x), \omega=\omega(x)$ of (7), for x on an open interval containing $x=0$, that satisfies $z(0)=\omega(0)=0$. so, there exists a solution branch $(x,y,c)=(x,y(x),c(x))$ of equation (6) that pass through this point $(0,y(0),c(0))=(0,y_0^*,c_0^*)$.

The solution $(x,y)=(x,y(x))$ is a fixed point of the composite equation (6) for $c=c(x)$ that corresponding to a 2-cycle point of the competition model (2). When $x = 0$, and hence $c = c_0^*$, $y = y_0^*$, this branch of 2-cycle intersects the exclusion cycle (5). For $x \geq 0$ the fixed point $(x, y) = (x, y(x)) \in R_+^2$ corresponds to a coexistence 2-cycle of (2). which means a branch of coexistence 2-cycle bifurcates from the exclusion 2-cycle (8) at $c = c^*$.

ACKNOWLEDGEMENTS

This work is financially supported by the major project of National Social Science Fund (12&ZD206); the National Natural Science Foundation of China (Project No. 90718038). Thanks for the help.

REFERENCES

1. T.Park, Experimental studies of interspecies competition. I. competition between populations of the four beetles Tribolium confusum Duval and Tribolium castaneum *Herbst, Ecol. Monogr.* 1948; **18**: 265-308
2. T.Park, Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of Tribolium, *physiol. zool*, 1954; **27**: 177-238
3. T.Park, Experimental studies of interspecies competition. III. Relation of initial species proportion to the competitive outcome in populations of Tribolium, *Physiol. Zool,* 1957; **30**: 22-40
4. T. Park, P.H.leslie and D.B.Mertz, Genetic strains and competition in populations of *Tribolium, Physiol. Zool*, 1964; **37**: 97-162
5. J.M.Cushing, Sheree Levarge, Nakul Chitnis and Shandelle Henson, Some discrete competition models and the competitive exclusion principle, *J.Diû.Equns.Appl*, 2004; **10**: 1139-1151.