

Difference Equations Arising in Evolutionary Population Dynamics

J. M. Cushing

Department of Mathematics
Interdisciplinary Program in Applied Mathematics
University of Arizona
Tucson, Arizona, USA

Simon Maccracken

Department of Ecology & Evolutionary Biology
University of Arizona
Tucson, Arizona, USA

Support by the
National Science Foundation



Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Density dependence

$$\left. \begin{array}{l} \varphi : \Omega \rightarrow \bar{\mathbb{R}}_+^1 = [0, +\infty) \\ \sigma : \Omega \rightarrow (0, 1) \end{array} \right\} \text{are } C^2$$

where $(0, 0) \in \Omega = \text{open} \subseteq \mathbb{R}^2$

$$\varphi(0, 0) = \sigma(0, 0) = 1$$

b = inherent (low density) adult fertility

s = inherent (low density) juvenile survival

$$R_0 \doteq sb$$

= inherent net reproductive number

(expected offspring per individual per life time)

OUTLINE

1. The basic juvenile-adult model in structured population dynamics & the Fundamental Bifurcation Theorem at $R_0 = 1$
2. Semelparity & the Dynamic Dichotomy
3. The Darwinian semelparous model (from evolutionary game theory) & the Dynamic Dichotomy
4. Examples: trade-offs, life history strategies & evolutionary stability
5. Summary & open problems

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

$$\left. \begin{array}{l} \varphi : \Omega \rightarrow \bar{\mathbb{R}}_+^1 = [0, +\infty) \\ \sigma_j, \sigma_a : \Omega \rightarrow (0, 1) \end{array} \right\} \text{are } C^2$$

where $(0, 0) \in \Omega = \text{open} \subseteq \mathbb{R}^2$

$$\varphi(0, 0) = \sigma_j(0, 0) = \sigma_a(0, 0) = 1$$

b = inherent adult fertility

s_j = inherent juvenile survival, $0 < s_a$ = inherent adult survival

$$R_0 \doteq \frac{s_j}{1 - s_a} b = \text{inherent net reproductive number}$$

(expected offspring per individual per life time)

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Define :

$$a_{\pm} \doteq \left[\partial_J^0 \sigma_j + \frac{s_j}{1-s_a} \partial_A^0 \varphi + \frac{s_a}{1-s_a} \frac{s_j}{1-s_a} \partial_A^0 \sigma_a \right] \pm \left[\partial_J^0 \varphi + \frac{s_j}{1-s_a} \partial_A^0 \sigma_j + \frac{s_a}{1-s_a} \partial_J^0 \sigma_a \right]$$

Within-class competitive effects

Between-class competitive effects

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Fundamental Bifurcation Theorem

1. Origin is stable if $R_0 < 1$ and unstable if $R_0 > 1$.

Assume $a_+ \neq 0$.

2. Positive equilibria (transcritically) bifurcate from the origin at $R_0 = 1$.

3. Stability depends on the direction of bifurcation:

Right (forward) bifurcating positive equilibria are **stable**.

Left (backward) bifurcating positive equilibria are **unstable**.

4. $a_+ < 0 \Rightarrow$ right (hence stable) bifurcation

$a_+ > 0 \Rightarrow$ left (hence unstable) bifurcation

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Notes

- A right (stable) bifurcation occurs if there are no positive feedback effects (at low density), i.e. if there are no positive derivatives $\partial_J^0 \sigma, \partial_A^0 \varphi, \partial_J^0 \varphi, \partial_A^0 \sigma$.
- Positive feedback terms (positive derivatives) are called *Allee effects*.
- A left (unstable) bifurcation can only occur in the presence of **strong** Allee effects.

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Lloyd & Dybas (1966, 1974)

Hoppensteadt & Keller (1976)

Bulmer (1977)

May (1979)

Ebenman (1987, 1988)

JC & Li (1989, 1992)

Wikan & (1996)

Nisbet & Onyiah (1994)

Wikan & Mjølhus (1997)

Behncke (2000)

Davydova (2004)

Davydova, Diekmann & van Gils (2003, 2005)

Mjølhus, Wikan & Solberg (2005)

JC (1991, 2003, 2006, 2010)

Kon (2005, 2007)

Diekmann & Yan (2008)

JC & Henson (2012)

Semelparity

Plants

Annuals



Monocarpic perennials



Invertebrates

Species of Insects
Arachnids
Molluscs



Periodical Insects



Magicicada spp.
13, 17 year cycles



Melantha spp.
3, 4, 5 year cycles

Vertebrates



Species of :

Fish
Lizards
Amphibians
Marsupials

... even a mammal !

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Define :

$$a_{\pm} \doteq [\partial_J^0 \sigma + s_j \partial_A^0 \varphi] \pm [\partial_J^0 \varphi + s_j \partial_A^0 \sigma]$$

Within-class competitive effects Between-class competitive effects

8/30

ICDEA 2012 Barcelona

10/30

ICDEA 2012 Barcelona

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Fundamental bifurcation Theorem

JC & Jia Li (1989), JC (2006), JC & Henson (2012)

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Fundamental bifurcation Theorem

1. Origin is stable if $R_0 = sb < 1$ and unstable if $R_0 > 1$.
Assume $a_+ \neq 0$.
2. Positive equilibria bifurcate from the origin at $R_0 = 1$.
 $a_+ < 0$ (or > 0) \Rightarrow right (or left) bifurcation
3. Synchronous 2-cycles also bifurcate from the origin at $R_0 = 1$.
 $\partial_J^0 \sigma + s \partial_A^0 \varphi < 0$ (or > 0) \Rightarrow right (or left) bifurcation
4. (a) Left bifurcations are unstable.
(b) A right bifurcation is stable if the other bifurcation is to the left.
(c) If both bifurcations are to the right, then

Dynamic Dichotomy

$a_- > 0 \Rightarrow$ equilibria stable & 2-cycles unstable

$a_- < 0 \Rightarrow$ equilibria unstable & 2-cycles stable

11/30

ICDEA 2012 Barcelona

11/30

ICDEA 2012 Barcelona

Notes

- If there are no Allee effects, that is, no positive derivatives

$$\partial_J^0 \sigma, \quad \partial_A^0 \varphi, \quad \partial_J^0 \varphi, \quad \partial_A^0 \sigma$$

then Dynamic Dichotomy occurs.

- Weak between-class competition gives stable equilibria

$$a_- \doteq [\partial_J^0 \sigma + s_j \partial_A^0 \varphi] - [\partial_J^0 \varphi + s_j \partial_A^0 \sigma] > 0$$

- Strong between-class competition gives stable synchronous 2-cycles

$$a_- \doteq [\partial_J^0 \sigma + s_j \partial_A^0 \varphi] - [\partial_J^0 \varphi + s_j \partial_A^0 \sigma] < 0$$

- Between-class (nymph) competition is leading hypothesis for periodical cicada dynamics

- Dichotomy observed in experiments with *Tribolium castaneum*

JC et al., *Chaos in Ecology*, Academic Press (2003)

King, Costantino, JC, Henson, Desharnais & Dennis, *Proc Nat Acad Sci* (2003)

Dennis, Desharnais, JC, Henson & Costantino, *Ecol Monogr* (2001)

Costantino, JC, Dennis & Desharnais, *Science* (1997)

12/30

ICDEA 2012 Barcelona

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u)\varphi(J_t, A_t, u)A_t \quad \varphi(0, 0, u) \equiv 1$$

$$A_{t+1} = s(u)\sigma(J_t, A_t, u)J_t \quad \sigma(0, 0, u) \equiv 1$$

u = mean of a phenotypic trait subject to Darwinian evolution

$u \in U$ = trait interval

Assume $\max_u \beta(u) = 1$.

Then b = maximum adult fertility (over the trait interval U)

14/30

ICDEA 2012 Barcelona

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Typical example for which the Dynamic Dichotomy occurs:

$$\sigma(J, A) = \frac{1}{1 + c_{11}J + c_{12}A}, \quad \varphi(J, A) = \frac{1}{1 + c_{21}J + c_{22}A}$$

Leslie-Gower-type competition interaction functionals

... a natural extension of discrete logistic
(or Beverton-Holt)

equation for an unstructured population.

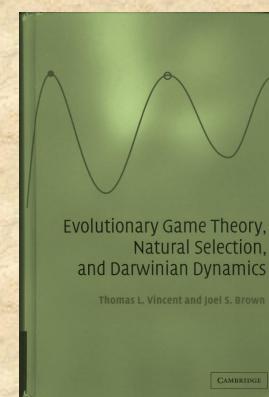
13/30

ICDEA 2012 Barcelona

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u)\varphi(J_t, A_t, u)A_t \quad \varphi(0, 0, u) \equiv 1$$

$$A_{t+1} = s(u)\sigma(J_t, A_t, u)J_t \quad \sigma(0, 0, u) \equiv 1$$



Vincent & Brown
2005

Using Evolutionary Game Theory
Methodology

$$u_{t+1} = u_t + \frac{1}{2}v \partial_u \ln R_0(J, A, u)$$

$$R_0(J, A, u) \doteq b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)$$

v = trait variance (assumed constant in time)

15/30

ICDEA 2012 Barcelona

Evolutionary Semelparous Juvenile-Adult Models

$$\begin{aligned} J_{t+1} &= b\beta(u_t)\varphi(J_t, A_t, u_t)A_t & \varphi(0, 0, u) &\equiv 1 \\ A_{t+1} &= s(u_t)\sigma(J_t, A_t, u_t)J_t & \sigma(0, 0, u) &\equiv 1 \\ u_{t+1} &= u_t + \frac{1}{2}\nu \partial_u \ln[b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)] \end{aligned}$$

- What are the dynamics of this model ?
- When $\nu = 0$ the Fundamental Bifurcation Theorem applies and the Dynamics Dichotomy is a possibility.
- What happens when $\nu > 0$ (i.e. when evolution is present)?

16/30

ICDEA 2012 Barcelona

Evolutionary Semelparous Juvenile-Adult Models

$$\begin{aligned} J_{t+1} &= b\beta(u_t)\varphi(J_t, A_t, u_t)A_t & \varphi(0, 0, u) &\equiv 1 \\ A_{t+1} &= s(u_t)\sigma(J_t, A_t, u_t)J_t & \sigma(0, 0, u) &\equiv 1 \\ u_{t+1} &= u_t + \frac{1}{2}\nu \partial_u \ln[b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)] \end{aligned}$$

Synchronous 2-cycles

$$\begin{pmatrix} J \\ 0 \\ u_1 \end{pmatrix} \leftrightarrow \begin{pmatrix} 0 \\ A \\ u_2 \end{pmatrix}$$

18/30

ICDEA 2012 Barcelona

Evolutionary Semelparous Juvenile-Adult Models

$$\begin{aligned} J_{t+1} &= b\beta(u_t)\varphi(J_t, A_t, u_t)A_t & \varphi(0, 0, u) &\equiv 1 \\ A_{t+1} &= s(u_t)\sigma(J_t, A_t, u_t)J_t & \sigma(0, 0, u) &\equiv 1 \\ u_{t+1} &= u_t + \frac{1}{2}\nu \partial_u \ln[b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)] \end{aligned}$$

Extinction Equilibria & Critical Traits

An extinction equilibrium (J, A, u) is an equilibrium with $J = A = 0$.

A critical trait u satisfies $\partial_u R_0(0, 0, u) = 0$.

Easy to see that ...

$(0, 0, u)$ is an extinction equilibrium if and only if u is a critical trait.

17/30

ICDEA 2012 Barcelona

Main Theorem

Assume ...

1. There exists a critical trait u^* : $\partial_u R_0(0, 0, u^*) = 0$
2. $\partial_{uu} R_0(0, 0, u^*) \neq 0$
3. $a_+ \doteq [\partial_J^0 \sigma + s_j \partial_A^0 \varphi] + [\partial_J^0 \varphi + s_j \partial_A^0 \sigma] \neq 0$ and $\partial_J^0 \sigma + s \partial_A^0 \varphi \neq 0$

Then ...

(a) If $\partial_{uu} R_0(0, 0, u^*) < 0$
then the Fundamental Bifurcation Theorem
and the Dynamic Dichotomy hold

... using $R_0(0, 0, u^*)$ as a bifurcation parameter.

(b) If $\partial_{uu} R_0(0, 0, u^*) > 0$
then the equilibria (extinction & positive) equilibria
and the synchronous 2-cycles
are all *unstable*.

NOTE: $R_0(0, 0, u) = b\beta(u)s(u)$

19/30

ICDEA 2012 Barcelona

Examples

Leslie-Gower Nonlinearities

$$\sigma(J, A) = \frac{1}{1 + c_{11}J + c_{12}A}, \quad \varphi(J, A) = \frac{1}{1 + c_{21}J + c_{22}A}$$

$$c_{ij} \geq 0, \quad \text{at least one } c_{ii} > 0$$

- No trait dependence in these density feedback terms
- No Allee effects
- Dynamic Dichotomy holds in absence of evolution
- Dynamic dichotomy holds occurs in the presence of evolution if
 $\partial_{uu}R_0(0, 0, u^*) < 0$

20/30

ICDEA 2012 Barcelona

Examples

$$J_{t+1} = b\beta(u_t) \frac{1}{1 + c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = s(u_t) \frac{1}{1 + c_{11}J_t + c_{12}A_t} J_t$$

$$u_{t+1} = u_t + \frac{1}{2} v \frac{\partial_u [\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0, 0, u) = b\beta(u)s(u)$$

Critical trait equation:

$$\partial_u^0 R_0(0, 0, u) = 0$$

$$\Leftrightarrow \beta'(u)s(u) + \beta(u)s'(u) = 0$$

Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0, 0, u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

Trade-offs are of fundamental biological interest:

Survival & fertility change in opposite manner as u increases.

Mathematically:

$s(u)$ and $\beta(u)$ have opposite monotonicity

21/30

ICDEA 2012 Barcelona

Examples

$$J_{t+1} = b\beta(u_t) \frac{1}{1 + c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = s(u_t) \frac{1}{1 + c_{11}J_t + c_{12}A_t} J_t$$

$$u_{t+1} = u_t + \frac{1}{2} v \frac{\partial_u [\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0, 0, u) = b\beta(u)s(u)$$

$$a_- \doteq [c_{21} + s(u^*)c_{12}] - [c_{11} + s(u^*)c_{22}] < 0$$

Critical trait equation:

$$\partial_u^0 R_0(0, 0, u) = 0$$

$$\Leftrightarrow \beta'(u)s(u) + \beta(u)s'(u) = 0$$

Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0, 0, u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

Stability critieria:

\Rightarrow stable equilibria

competition ratio

Examples

$$J_{t+1} = b\beta(u_t) \frac{1}{1 + c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = s(u_t) \frac{1}{1 + c_{11}J_t + c_{12}A_t} J_t$$

$$u_{t+1} = u_t + \frac{1}{2} v \frac{\partial_u [\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0, 0, u) = b\beta(u)s(u)$$

$c < 1 \Rightarrow$ stable equilibria

Critical trait equation:

$$\partial_u^0 R_0(0, 0, u) = 0$$

$c > 1 \Rightarrow$ stable 2-cycles

Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0, 0, u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

22/30

ICDEA 2012 Barcelona

ICDEA 2012 Barcelona

Example 1

$$J_{t+1} = b \frac{1}{1+u_t} \frac{1}{1+c_{21}J_t + c_{22}A_t} A_t$$

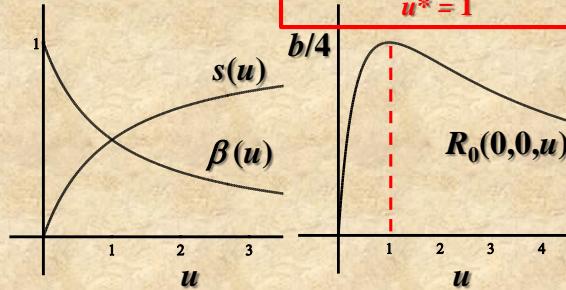
$$A_{t+1} = \frac{u_t}{1+u_t} \frac{1}{1+c_{11}J_t + c_{12}A_t} J_t$$

$$u_{t+1} = u_t + \frac{1}{2} v \frac{1-u_t}{(1+u_t)u_t}$$

$$s(u) = \frac{u}{1+u}, \quad \beta(u) = \frac{1}{1+u}$$

trait interval: $U = [0, +\infty)$

$$R_0(0,0,u) = b \frac{u}{(1+u)^2}$$



23/30

ICDEA 2012 Barcelona

Example 1

Sample Time Series

$$R_0(0,0,1) = 0.75$$

Extinction

$$R_0(0,0,1) = 2$$

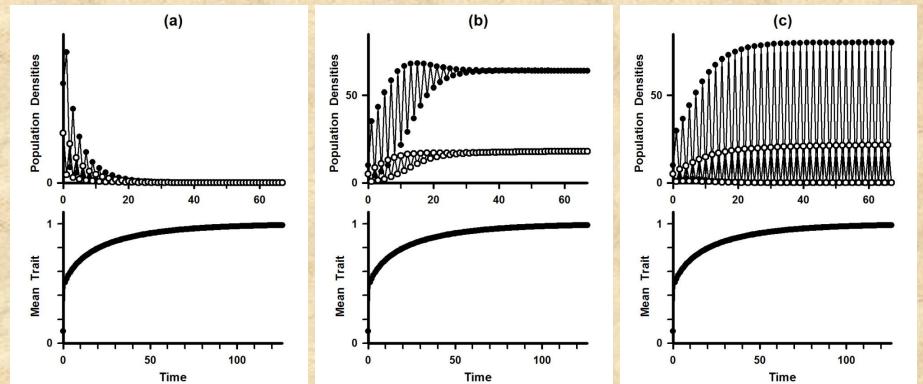
$c < 1$

Stable Equilibrium

$$R_0(0,0,1) = 2$$

$c > 1$

Stable 2-cycle



24/30

ICDEA 2012 Barcelona

Example 2

$$J_{t+1} = b \frac{2\varepsilon + u_t^2}{2 + u_t^2} \frac{1}{1+c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = \frac{2m}{1+au_t^2} \frac{1}{1+c_{11}J_t + c_{12}A_t} J_t$$

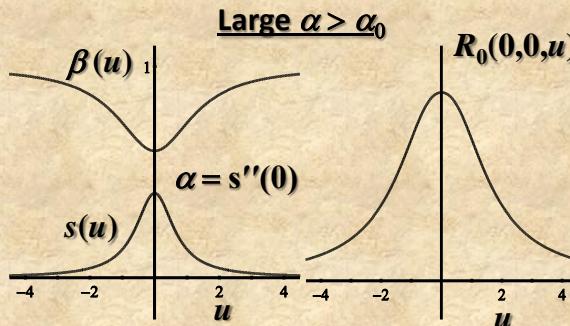
$$u_{t+1} = u_t - vu \frac{1+2\alpha+2\alpha u_t^2}{(1+\alpha u_t^2)(1+u_t^2)}$$

$$s(u) = \frac{2m}{1+au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

$\alpha > 0, \quad 0 < m, \varepsilon < 1$

trait interval: $U = R^1$

$$R_0(0,0,u) = b \frac{2m}{1+au^2} \frac{2\varepsilon + u^2}{2 + u^2}$$



25/30

ICDEA 2012 Barcelona

Example 2

$$J_{t+1} = b \frac{2\varepsilon + u_t^2}{2 + u_t^2} \frac{1}{1+c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = \frac{2m}{1+au_t^2} \frac{1}{1+c_{11}J_t + c_{12}A_t} J_t$$

$$u_{t+1} = u_t - vu \frac{1+2\alpha+2\alpha u_t^2}{(1+\alpha u_t^2)(1+u_t^2)}$$

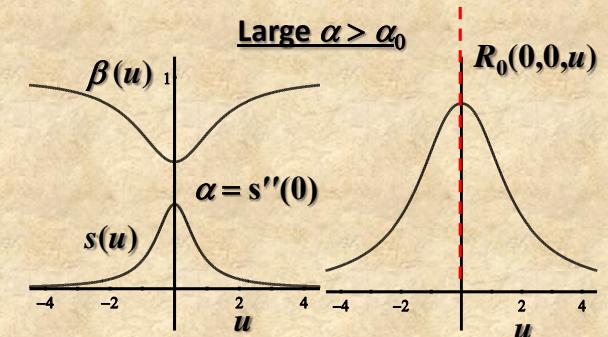
Dynamical Dichotomy holds at critical trait $u^* = 0$

$$s(u) = \frac{2m}{1+au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

$\alpha > 0, \quad 0 < m, \varepsilon < 1$

trait interval: $U = R^1$

$$R_0(0,0,u) = b \frac{2m}{1+au^2} \frac{2\varepsilon + u^2}{2 + u^2}$$



25/30

ICDEA 2012 Barcelona

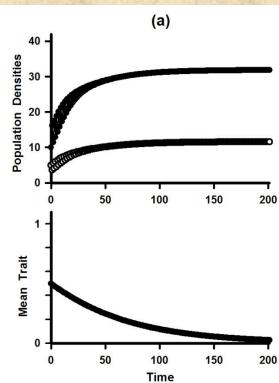
Example 1

Sample Time Series

$$R_0(0,0,0) = 1.5$$

$c < 1$

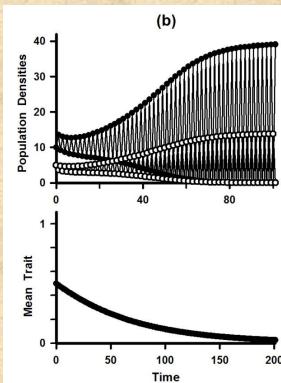
Stable Equilibrium



$$R_0(0,0,0) = 1.5$$

$c > 1$

Stable 2-cycle



26/30

ICDEA 2012 Barcelona

Example 2

$$J_{t+1} = b \frac{2\varepsilon + u_t^2}{2 + u_t^2} \frac{1}{1 + c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = \frac{2m}{1 + au_t^2} \frac{1}{1 + c_{11}J_t + c_{12}A_t} A_t$$

$$u_{t+1} = u_t - vu \frac{1 + 2\alpha + 2\alpha u_t^2}{(1 + \alpha u_t^2)(1 + u_t^2)}$$

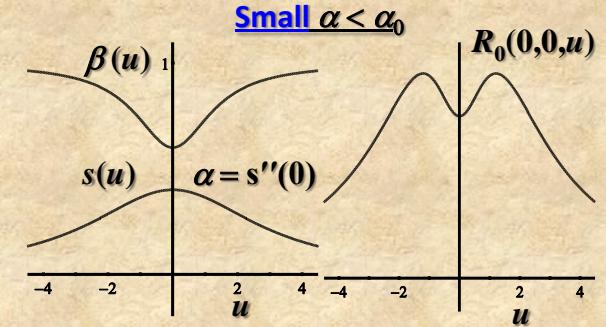
Small $\alpha < \alpha_0$

$$s(u) = \frac{2m}{1 + au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

$\alpha > 0, \quad 0 < m, \varepsilon < 1$

trait interval : $U = R^1$

$$R_0(0,0,u) = b \frac{2m}{1 + au^2} \frac{2\varepsilon + u^2}{2 + u^2}$$



27/30

ICDEA 2012 Barcelona

Example 2

$$J_{t+1} = b \frac{2\varepsilon + u_t^2}{2 + u_t^2} \frac{1}{1 + c_{21}J_t + c_{22}A_t} A_t$$

$$A_{t+1} = \frac{2m}{1 + au_t^2} \frac{1}{1 + c_{11}J_t + c_{12}A_t} A_t$$

$$u_{t+1} = u_t - vu \frac{1 + 2\alpha + 2\alpha u_t^2}{(1 + \alpha u_t^2)(1 + u_t^2)}$$

Dynamical Dichotomy
holds at
2 critical traits $\pm u^*$

Example 2

Sample Time Series

$$R_0(0,0,u^*) = 1.5$$

$c < 1$
Stable Equilibrium

$$R_0(0,0,u^*) = 1.5$$

$c > 1$
Stable 2-cycle

$$s(u) = \frac{2m}{1 + au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

$\alpha > 0, \quad 0 < m, \varepsilon < 1$

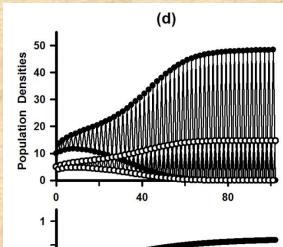
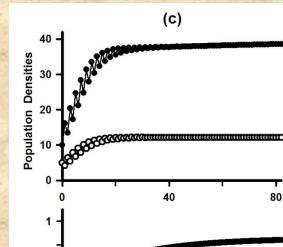
trait interval : $U = R^1$

$$R_0(0,0,u) = b \frac{2m}{1 + au^2} \frac{2\varepsilon + u^2}{2 + u^2}$$

Small $\alpha < \alpha_0$

$\alpha = s''(0)$

u will
equilibrate
at negative
critical trait
for other
initial
conditions



27/30

ICDEA 2012 Barcelona

28/30

ICDEA 2012 Barcelona

Summary

For the EGT semelparous juvenile-adult model :

- The Fundamental Bifurcation Theorem holds at critical traits u^* where inherent (low density) fitness has a local maximum :

$$\partial_u R_0(0,0,u^*) = 0, \quad \partial_{uu} R_0(0,0,u^*) < 0$$

- Positive equilibria & synchronous 2-cycles bifurcate at $R_0(0,0,u^*) = 1$.

- The Dynamic Dichotomy holds.

For example, when no Allee effects are present.

Open Problems

- What are the properties of the bifurcation at $R_0 = 1$ for Leslie semelparous of **dimensions 3 and higher** without evolution ? with evolution?

- Global stability results? Especially for Leslie-Gower nonlinearities.

- What happens to bifurcating branches for large $R_0 \gg 1$?

- EGT Leslie semelparous models with **2 or more phenotypic traits**