Matrix Models for the Darwinian Dynamics of Structured Populations
Applications to the Threat of Extinction from Climate Change

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Glaucous-winged Gulls

Sentinels of climate change
Glaucous-wing gull (*Larus glaucescens*). Colonies of ~70,000 nesting birds are located on Protection Island. ~ 75% in Puget Sound area.
1. Increased mean sea surface temperature correlates with increased egg cannibalism


“a 0.1 °C rise in SST is associated with a 10% increase in the odds that an egg is cannibalized”
Presumably, continued increased in SST will result in increased egg cannibalism.

Is cannibalism a sustainable strategy for long term survival?
1. Increased mean sea surface temperature correlates with increased egg cannibalism

2. Increased mean sea surface temperature correlates every-other-day ovulation synchrony


1. Increased mean sea surface temperature correlates with increased egg cannibalism

2. Increased mean sea surface temperature correlates every-other-day ovulation synchrony

- Why is this? Related to increased egg cannibalism?

- What role does this play in the long term adaptation to increased SST?
Some questions on which we have focused:

- Can a population headed for extinction -- due to decreased environmental resource availability -- survive by engaging in cannibalism?

- Can cannibalism be selected by Darwinian principles? (i.e. be an ESS)

- Might female reproductive synchrony be a dynamic that results from egg cannibalism?

- What role does a fluctuating environment play? Random versus regular (such as El Niño events)
Models of increasing complexity

(as more biological features of the motivating gull breeding colony are incorporated)

1. 2D Juvenile-Adult cannibalism models
   Use of available bifurcation theorems & methods

   Basic question: extinction or survival?

   What occurs when the extinction state destabilizes
   when a model parameter is manipulated?
Models of increasing complexity
(as more biological features of the motivating gull breeding colony are incorporated)

1. 2D Juvenile-Adult cannibalism models
   Use of available bifurcation theorems & methods

2. Evolutionary (EGT) versions of 2D models
   Straightforward, but nontrivial generalization of bifurcation theorems

3. Periodically forced 2D EGT models
   Bifurcation theory in progress ...

4. Higher dimensional, structured population models to study reproductive synchrony
   Needed to prove new bifurcation theorems

5. Higher dimensional, periodic models to address disparate time scales
A quick word about proofs ...

Equation for equilibrium or periodic solutions is placed in the form

\[ u = \lambda Lu + H(u, \lambda) \]

\[ u \in B = \text{Banach space}, \lambda = \text{real}, L = \text{linear compact} \]

\[ H = \text{completely continuous} \]

\[ = O(\|u\|^2) \text{ near } u = 0 \text{ uniformly on compact } \lambda \text{ sets} \]

Make use of

Taylor expansions, Fredholm alternative, Green’s functions, Perron-Frobenius theory, ...
A quick word about proofs ... 

\[ u = \lambda Lu + H(u, \lambda) \]

Characteristic values: \( 0 \neq u = \lambda_0 Lu \)

Local bifurcations: classical local bifurcation & stability methods (Krasnoselski, Liapunov-Schmidt methods, ... )

\[ \lambda_0 = \text{geometrically simple} \]
A quick word about proofs ...

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Local bifurcations: classical local bifurcation & stability methods
(\textit{Krasnoselski, Liapunov-Schmidt methods, ...})

Stability depends on direction of bifurcation
(\textit{Exchange of Stability Principle for Transcritical Bifurcations})

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A quick word about proofs ...

\[ u = \lambda Lu + H(u, \lambda) \]

Characteristic values: \( 0 \neq u = \lambda_0 Lu \)

Local bifurcations: classical local bifurcation & stability methods
   (Krasnoselski, Liapunov-Schmidt methods, ... )

Global bifurcations: connect to \( \infty \) or another \( \lambda_0 \) of odd multiplicity
   (Rabinowitz & Crandall)

\[ \lambda_0 = \text{geometrically simple} \]
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

\[ \hat{x}(t + 1) = P \hat{x}(t) \]

\[ \hat{x} = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \]

Time unit = maturation period

\[ P = \begin{pmatrix} 0 & b \\ s_1 & s_2 \end{pmatrix} \]

\[ b > 0, \quad 0 \leq s_i \leq 1 \]
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Negative effect of adult cannibalism on juvenile survival

\[
P(\hat{x}) = \begin{pmatrix} 0 & b \\ s_1 \sigma(x_1, x_2) & s_2 \end{pmatrix}
\]

\[ b > 0, \quad 0 \leq s_i \leq 1 \]

Time unit = maturation period
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Time unit = maturation period

Negative effect of adult cannibalism on juvenile survival

Positive effect of adult cannibalism on adult survival

\[ P(\hat{x}) = \begin{pmatrix} 0 & b \\ s_1 \sigma_1(x_1, x_2) & s_2 \sigma_2(x_1, x_2) \end{pmatrix} \]

\[ b > 0, \quad 0 \leq s_i \leq 1 \]
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

\[ \hat{x}(t + 1) = P(\hat{x}(t))\hat{x}(t) \]

\( P(\hat{x}) \) is non-negative, irreducible, primitive & smooth in \( \hat{x} \)

\[ r(\hat{x}) = \rho[P(\hat{x})] \] is the spectral radius of \( P(\hat{x}) \)

**Juvenile-Adult Model**

\[ r_0 = \frac{1}{2} \left( s_2 + \sqrt{s_2^2 + 4bs_1} \right) \]

inherent population growth rate

\[ R_0 = \frac{bs_1}{1 - s_2} \]

inherent net reproduction number
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

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\[ r(\hat{x}) = \rho[P(\hat{x})] \] is the spectral radius of \( P(\hat{x}) \)

- \( \hat{x} \in \mathbb{R}_+^n \)
- \( \kappa < 0 \) \quad \text{stable}
- \( \kappa > 0 \) \quad \text{unstable}

Direction of bifurcation is determined by the sign of a diagnostic quantity

\[ \kappa = \text{non-negative linear combination of } \partial_k p_{ij}(\hat{0}) \]
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- \( \hat{x} \in R^n \)
- \( \kappa < 0 \)
- Forward bifurcation
- Negative density effects are dominant at low density

- \( \hat{x} \in R^n \)
- \( \kappa > 0 \)
- Backward bifurcation
- Positive density effects are dominant at low density
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

\[ \hat{x}(t+1) = P(\hat{x}(t))\hat{x}(t) \]

\(P(\hat{x})\) is non-negative, irreducible, primitive & smooth in \(\hat{x}\)

\[ r(\hat{x}) = \rho[P(\hat{x})] \] is the spectral radius of \(P(\hat{x})\)

\(\hat{x} \in R^n_+\)

**Negative feedback at high density**

**Forward bifurcation**

*Negative* density effects are dominant at low density

**Backward bifurcation**

*Positive* density effects are dominant at low density
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

\[ \hat{x}(t + 1) = P(\hat{x}(t))\hat{x}(t) \]

\( P(\hat{x}) \) is non-negative, irreducible, primitive & smooth in \( \hat{x} \)

\[ r(\hat{x}) = \rho[P(\hat{x})] \] is the spectral radius of \( P(\hat{x}) \)

Strong Allee Effect
Multiple attractors
1 of which is extinction
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

Cannibalism produces negative and positive feedbacks.

$r_0 < 1$ means degraded environment.

$\hat{x} \in R^n$  

Non-cannibal

Stable

Unstable

$r_0$ or $R_0$

Cannibal

Stable

Unstable

$r_0$ or $R_0$

Cannibalism produces negative and positive feedbacks.
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

- $r_0 < 1$ means degraded environment

- $x \in R^n$

- Non-cannibal

- Cannibal

- Possible survival, but...
  - still endangered (by Allee basin)
  - beware of tipping point
1. Highlights of a Basic Juvenile-Adult Cannibalism Model

Can population get from here to there by Darwinian natural selection?

That is, can evolution select for cannibalism?

$r_0 < 1$ means degraded environment

$\hat{x} \in R^n$

Cannibal

Non-cannibal
Models of increasing complexity
( as more biological features of the motivating gull breeding colony are incorporated )

✓ 1. 2D Juvenile-Adult cannibalism models
   Use of available bifurcation theorems & methods

2. Evolutionary (EGT) versions of 2D models
   Straightforward, but nontrivial generalization of bifurcation theorems

3. Periodically forced 2D EGT models
   Bifurcation theory in progress ...

4. Higher dimensional, structured population models to study reproductive synchrony
   Needed to prove new bifurcation theorems
Evolutionary (Darwinian) Dynamics

\[ \hat{x}(t + 1) = P(\hat{x}(t), u(t), \nu) \bigg|_{\nu = u(t)} \hat{x}(t) \]

- \( \nu \) = a phenotypic trait subject to axioms of Darwinian evolution
- \( u \) = mean phenotypic trait in the population

Evolutionary Game Theory

Vincent & Brown
Cambridge U Press 2005
Evolutionary (Darwinian) Dynamics

\[
\hat{x}(t + 1) = P(\hat{x}(t), u(t), \nu)|_{\nu = u(t)} \hat{x}(t)
\]

\[
u(t + 1) = u(t) + \sigma^2 \partial_{\nu} f(\hat{x}(t), u(t), \nu)|_{\nu = u(t)}
\]

- \(\nu\) = a phenotypic trait subject to axioms of Darwinian evolution
- \(u\) = mean phenotypic trait in the population

The Breeder’s equation (Lush 1937)

or

Lande’s equation

or

Fisher’s equation of additive genetic variance

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Evolutionary (Darwinian) Dynamics

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- \( \nu \) = a phenotypic trait subject to axioms of Darwinian evolution
- \( u \) = mean phenotypic trait in the population
- \( f(\hat{x}, u, \nu) \) = "fitness"
- \( \sigma^2 \) is related to phenotypic variance, assumed constant (measures the speed of evolution)

Evolutionary Game Theory

Vincent & Brown

Cambridge U Press 2005
Evolutionary (Darwinian) Dynamics

\[ \hat{x}(t + 1) = P(\hat{x}(t), u(t), v) \big|_{v=u(t)} \hat{x}(t) \]

\[ u(t + 1) = u(t) + \sigma^2 \frac{\partial}{\partial v} f(\hat{x}(t), u(t), v) \big|_{v=u(t)} \]

Commonly used fitness functions

\[ f(\hat{x}, u, v) = \ln r(\hat{x}, u, v) \text{ or } r(\hat{x}, u, v) \text{ or } R_0(\hat{x}, u, v) \]
Evolutionary (Darwinian) Dynamics

\[
\hat{x}(t+1) = P(\hat{x}(t), u(t), v)|_{v=u(t)} \hat{x}(t)
\]

\[
u(t+1) = u(t) + \sigma^2 \partial_v f(\hat{x}(t), u(t), v)|_{v=u(t)}
\]

Same bifurcation results have been established

JC (2010); JC & Stump (2013); JC, Henson & Hayward; Meissen, Salau & JC (2016)

assuming there exists a critical trait \( u^* \):

\[
\partial_v f(\hat{0}, u^*, v)|_{v=u^*} = 0
\]

which implies there exists

an extinction equilibrium

\((\hat{x}, u^*) = (\hat{0}, u^*)\)
Evolutionary (Darwinian) Dynamics

\[ \hat{x}(t + 1) = P(\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \hat{x}(t) \]

\[ u(t + 1) = u(t) + \sigma^2 \partial_v f (\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \]

Same bifurcation results have been established
JC (2010); JC & Stump (2013); JC, Henson & Hayward; Meissen, Salau & JC (2016)

assuming there exists a critical trait \( u^* \):

\[ \partial_v f (\hat{0}, u^*, v) \bigg|_{v=u^*} = 0 \quad \text{and} \quad \partial_v^2 f (\hat{0}, u^*, v) \bigg|_{v=u^*} < 0 \]

\[ r_0 = r(\hat{0}, u^*, u^*) \quad \text{or} \quad R_0(\hat{0}, u^*, u^*) \quad \text{is used as the bifurcation parameter.} \]

JC, On the relationship between \( r \) and \( R_0 \) and its role in the bifurcation of equilibria of Darwinian matrix models, J Biol Dynamics 5 (2011)
Evolutionary (Darwinian) Dynamics

$$\hat{x}(t + 1) = P(\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \hat{x}(t)$$

$$u(t + 1) = u(t) + \sigma^2 \partial_v f(\hat{x}(t), u(t), v) \bigg|_{v=u(t)}$$

Same bifurcation results have been established
JC (2010); JC & Stump (2013); JC, Henson & Hayward; Meissen, Salau & JC (2016)

Bifurcation of positive equilibrium pairs \((\hat{x}, u), \hat{x} \in R^+\)

Direction of bifurcation is determined by the sign of a diagnostic quantity

$$\kappa = \text{non-negative linear combination of } \partial_k p_{ij}(\hat{0}, u^*, u^*)$$
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, \nu) = \begin{pmatrix} 0 & \text{Adult fertility} \\ s_1(1 - \psi(\hat{x}, \nu) x_2) & s(\psi(\hat{x}, \nu) x_1) \end{pmatrix} \]

Juvenile survival  Adult survival

Diagram showing the flow between Juveniles and Adults with labels for `b`, `s_1`, and `s_2`.
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\phi(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

\[ \rho = \text{available environmental resource} \]
Inherent fertility rate depends on

- environment resource availability $\rho$
- a trait subject to evolution $v$.

For example:

\[
b(v, \rho) = b m(v) \frac{\rho}{1 + \rho}
\]
2. EGT Juvenile-Adult Cannibalism Model

\[
P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho) \rho(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix}
\]

Holling II resource uptake rate depends on the trait \( v \).

Inherent fertility rate depends on
- environment resource availability \( \rho \)
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Resource to offspring conversion factor
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho) \rho(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

Holling II resource uptake rate depends on the trait \( v \).

For example

\[ m(v) = \exp(-v^2 / 2 w_m^2) \]

Maximal resource uptake at trait \( v = 0 \)

Inherent fertility rate depends on

- environment resource availability \( \rho \)
- a trait subject to evolution \( v \).

For example

\[ b(v, \rho) = b m(v) \frac{\rho}{1 + \rho} \]
2. EGT Juvenile-Adult Cannibalism Model

\[
P(\hat{x}, \nu) = \begin{pmatrix}
0 & b(\nu, \rho)\phi(x_2) \\
\frac{s_1(1 - \psi(\hat{x}, \nu, \rho)x_2)}{s(\psi(\hat{x}, \nu, \rho)x_1)} & s(\psi(\hat{x}, \nu, \rho)x_1)
\end{pmatrix}
\]

Probability a juvenile is cannibalized depends on

- environment resource availability \( \rho \)
- a trait subject to evolution \( \nu \)
- population density \( \hat{x} \).
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\varphi(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

Probability a juvenile is cannibalized depends on

- environment resource availability \( \rho \)
- a trait subject to evolution \( v \)
- population density \( \hat{x} \).

For example

\[ \psi(\hat{x}, v, \rho)x_2 = \frac{1}{1 + c_4 \rho} \frac{1}{1 + c_3 x_1} \frac{w(v)}{1 + w(v)x_2} x_2 \]
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\varphi(x_2) \\ s(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

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Cannibalism activity inversely related to environmental resource availability

For example
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\phi(x_2) \\ s_1(1-\psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

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Predator saturation effect by prey
2. EGT Juvenile-Adult Cannibalism Model

\[
P(\hat{x}, v) = \begin{pmatrix}
0 & b(v, \rho)\varphi(x_2) \\
\frac{s_1(1 - \psi(\hat{x}, v, \rho)x_2)}{s(\psi(\hat{x}, v, \rho)x_1)} & s(\psi(\hat{x}, v, \rho)x_1)
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Probability a juvenile is cannibalized depends on

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\[
\psi(\hat{x}, v, \rho)x_2 = \frac{1}{1 + c_4 \rho} \frac{1}{1 + c_3 x_1} \frac{w(v)}{1 + w(v)x_2} x_2
\]

Holling II predator-prey functional response

A negative density effect
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\phi(x_2) \\ s_1(1-\psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

Probability a juvenile is cannibalized depends on
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Holling II predator-prey functional response

Trait \( v \) determines cannibalism intensity \( w(v) \)
2. EGT Juvenile-Adult Cannibalism Model

\[
P(\hat{x},v) = \begin{pmatrix}
0 & b(v, \rho)\phi(x_2) \\
\rho \cdot s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1)
\end{pmatrix}
\]

Probability a juvenile is cannibalized depends on

- environment resource availability \( \rho \)
- a trait subject to evolution \( v \)
- population density \( \hat{x}. \)

For example

\[
\psi(\hat{x}, v, \rho)x_2 = \frac{1}{1 + c_4 \rho} \frac{1}{1 + c_3 x_1} \frac{w(v)}{1 + w(v)x_2} x_2
\]

Maximal cannibalism intensity at trait \( v = 1 \)

\[
w(v) = \omega \exp(\frac{(v - 1)^2}{2a_w^2})
\]
2. EGT Juvenile-Adult Cannibalism Model

\[
P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\varphi(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix}
\]

Adult survival probability is an increasing function of the number of cannibalized juveniles

\[
s(z) = \psi(\hat{x}, v, \rho)x_1
\]

A positive density effect.
2. EGT Juvenile-Adult Cannibalism Model

\[ P(\hat{x}, v) = \begin{pmatrix} 0 & b(v, \rho)\varphi(x_2) \\ s_1(1 - \psi(\hat{x}, v, \rho)x_2) & s(\psi(\hat{x}, v, \rho)x_1) \end{pmatrix} \]

There is a unique critical trait at which \( r(\hat{0}, v) \) has a local maximum, namely \( v^* = 0 \).

The alternatives of the the bifurcation theorem apply.


Simulation Examples

Resource availability: $\rho = 10$

Cannibalism: $\omega = 0$ (off)

Initial conditions: $x_1 = 0$, $x_2 = 1$, $u = 1.5$

Inherent growth rate: $r_0 = 1.27 > 1$

Direction of bifurcation: $\kappa = 0.01 > 0$ (forward)

trait maximizes resource uptake
Simulation Examples

Resource availability: $\rho = 10$

Cannibalism: $\omega = 0$ (off)

Initial conditions: $x_1 = 0$, $x_2 = 1$, $u = 1.5$

Inherent growth rate: $r_0 = 1.27 > 1$

Direction of bifurcation: $\kappa = 0.01 > 0$ (forward)

Global maximum

ESS Maximum Principle implies $u = 0$ is an ESS

trait maximizes resource uptake
Simulation Examples

Resource availability: \( \rho = 0.3 \)

Cannibalism: \( \omega = 0 \) (off)

Initial conditions: \( x_1 = 0, \ x_2 = 1, \ u = 1.5 \)

Inherent growth rate: \( r_0 = 0.81 < 1 \)

Direction of bifurcation: \( \kappa = 0.01 > 0 \) (forward)
Simulation Examples

Resource availability: \( \rho = 0.3 \)

Cannibalism: \( \omega = 0 \) (off)

Initial conditions: \( x_1 = 0, \ x_2 = 1, \ u = 1.5 \)

Inherent growth rate: \( r_0 = 0.81 < 1 \)

Direction of bifurcation: \( \kappa = 0.01 > 0 \) (forward)

\[ \ln r(\hat{x}_t, \upsilon) \]

extinction
Simulation Examples

Resource availability: $\rho = 0.3$

Cannibalism: $\omega = 10$ (on)

Inherent growth rate: $r_0 = 0.81 < 1$

Direction of bifurcation: $\kappa = -509 < 0$ (backward)

Initial conditions: $x_1 = 0, x_2 = 1, u = 1.5$
Simulation Examples

Resource availability: $\rho = 0.3$

Cannibalism: $\omega = 10$ (on)

Initial conditions: $x_1 = 0$, $x_2 = 1$, $u = 1.5$

Inherent growth rate: $r_0 = 0.81 < 1$

Direction of bifurcation: $\kappa = -509 < 0$ (backward)

Evolution selects in favor of more cannibalism.

Global maximum

ESS Maximum Principle implies $u = 0.45$ is an ESS
Simulation Examples

Resource availability: $\rho = 0.3$  
Inherent growth rate: $r_0 = 0.81 < 1$

Cannibalism: $\omega = 10$ (on)  
Direction of bifurcation: $\kappa = -509 < 0$ (backward)

Initial conditions: $x_1 = 0, \ x_2 = 1, \ u = 1.5$  

Strong Allee Effect

Survival is initial condition dependent
Simulation Examples

Resource availability: $\rho = 0.3$

Cannibalism: $\omega = 10$ (on)

Initial conditions: $x_1 = 0, x_2 = 1, u = 2.0$

Inherent growth rate: $r_0 = 0.81 < 1$

Direction of bifurcation: $\kappa = -509 < 0$ (backward)

![Graphs showing extinction and fitness landscape](image-url)
Simulation Examples

Resource availability: $\rho = 10$

Cannibalism: $\omega = 10$ (on)

Inherent growth rate: $r_0 = 1.27 > 1$

Initial conditions: $x_1 = 0, \quad x_2 = 1, \quad u = 2.0$

Direction of bifurcation: $\kappa = -60.15 < 0$ (backward)

Environmental resource availability recovers
Simulation Examples

- Resource availability: \( \rho = 10 \)
- Cannibalism: \( \omega = 10 \) (on)
- Initial conditions: \( x_1 = 0, \ x_2 = 1, \ u = 2.0 \)
- Inherent growth rate: \( r_0 = 1.27 > 1 \)
- Direction of bifurcation: \( \kappa = -60.15 < 0 \) (backward)

![Graph showing survival over time](image1)

**trait maximizes resource uptake**

![Graph showing fitness landscape](image2)
Some Punch Lines from this EGT JA Cannibalism Model

Evolution selects

• against cannibalism in a good environment
• for cannibalism in a bad environment

But what if the environment is not constant?

• regularly occurring bad years
• or stochastic fluctuations between good & bad years
A List of models of increasing complexity as more biological features of the motivating gull breeding colony are incorporated

1. 2D Juvenile-Adult cannibalism model
   Use of available bifurcation methods

2. Evolutionary (EGT) version of 2D model
   Straightforward, but nontrivial generalization of bifurcation theorems

3. Periodically forced 2D EGT model
   Bifurcation theory in progress ...

4. Higher dimensional, structured population models to include reproductive synchrony
   Needed to prove non-generic bifurcation theorems
3. EGT JA Cannibalism Model in a Periodic Environment

\[
P(t, \hat{x}, v) = \begin{pmatrix}
0 & b(v, \rho_t)\phi(x_2) \\
 s_1(1 - \psi(\hat{x}, v, \rho_t)x_2) & s(\psi(\hat{x}, v, \rho_t)x_1)
\end{pmatrix}
\]

\[\rho_t = \text{environmental resource availability is periodic in } t\]

The bifurcation theorem described above has been extended

- to periodically forced matrix models (JC, 2006 & 1998)

and is

- currently being worked out for EGT versions.
Simulation Examples

One of the earlier examples:

- Cannibalism present
- $r_0 > 1$
- Evolution selects against cannibalism
Simulation Examples

**CONSTANT**

Evolution selects against cannibalism

**PERIODIC**

Evolution selects for cannibalism

A good year - bad year scenario
Simulation Examples

**CONSTANT**
- Evolution selects *against* cannibalism

**PERIODIC**
- Evolution selects *for* cannibalism

**RANDOM**
- 50-50 chance that next year is good or bad
Simulation Examples

**CONSTANT**

Evolution selects **against** cannibalism

**PERIODIC**

Evolution selects **for** cannibalism

**RANDOM**

Evolution selects **against** cannibalism
Simulation Examples

It has been observed in laboratory experiments with nematodes (*Caenorhabditis elegans*)
Dey et al., PLOS Biology 2016

This phenomenon contradicts the popular “bet hedging” principle.

Evolution selects *for* cannibalism

Evolution selects *against* cannibalism
A List of models of increasing complexity as more biological features of the motivating gull breeding colony are incorporated

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4. Highlights of a Cannibalism & Reproductive Synchrony Model

\[ P(\hat{x}) = \begin{pmatrix} 0 & b \beta(\hat{x}) & 0 \\ s_1 \sigma_1(\hat{x}) & 0 & s_3 g(x_2) \sigma_3(\hat{x}) \\ 0 & s_2 \sigma_2(\hat{x}) & s_3 (1 - g(x_2)) \sigma_3(\hat{x}) \end{pmatrix} \]
4. Highlights of a Cannibalism & Reproductive Synchrony Model

In absence of density effects, a female returns to reproductive activity after 1 time unit.
4. Highlights of a Cannibalism & Reproductive Synchrony Model

$$P(\hat{x}) = \begin{pmatrix}
0 & b\beta(\hat{x}) & 0 \\
s_1\sigma_1(\hat{x}) & 0 & s_3g(x_2)\sigma_3(\hat{x}) \\
0 & s_2\sigma_2(\hat{x}) & s_3(1 - g(x_2))\sigma_3(\hat{x})
\end{pmatrix}$$

$g(x_2)$ a decreasing function with $g(0) = 1$

$$P(\hat{0}) = \begin{pmatrix}
0 & b & 0 \\
s_1 & 0 & s_3 \\
0 & s_2 & 0
\end{pmatrix}$$
is imprimitive
\[
\hat{x}(t+1) = P(\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \hat{x}(t)
\]

\[
u(t+1) = u(t) + \sigma^2 \partial_v f(\hat{x}(t), u(t), v) \bigg|_{v=u(t)}
\]

If \( P(\hat{0}, v^*) \) is imprimitive, the bifurcation at \( r_0 = 1 \) changes in significant ways

- Branches of other invariant sets (e.g. synchronous cycles) bifurcate in addition to positive equilibria
  (Synchronous cycle = periodic cycle on the boundary of the positive cone)

- Direction of bifurcation no longer determines stability
\[ \hat{x}(t+1) = P(\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \hat{x}(t) \]
\[ u(t+1) = u(t) + \sigma^2 \partial_v f(\hat{x}(t), u(t), v) \bigg|_{v=u(t)} \]

If \( P(\hat{0}, v^*) \) is imprimitive,

the bifurcation at \( r_0 = 1 \) changes in significant ways.

General case is little understood.

Two classes of imprimitive matrices for which results are known:

- **Semelparous Leslie Matrices**
  (used to study dynamics of periodical insects, e.g. periodical cicadas)

- **Beta Matrices**
  (A. Veprauskas, PhD dissertation, U of Arizona, 2016)
4. Highlights of a Cannibalism & Reproductive Synchrony Model

Veprauskas’ Theorem

Assume there exists a critical trait. Two continua bifurcate at $r_0 = 1$:

- Positive equilibria
- Synchronous 2-cycles
Veprauskas’ Theorem

Assume there exists a critical trait. **Two** continua bifurcate at $r_0 = 1$:

- Positive equilibria
- Synchronous 2-cycles

\[
\begin{pmatrix}
\text{juveniles} \\
\text{active adults} \\
\text{inactive adults} \\
\text{trait}
\end{pmatrix}
+ \begin{pmatrix}
+
+
+
u_e
\end{pmatrix}
= \begin{pmatrix}
0 \\
+ \\
0 \\
u_1 \\
u_2
\end{pmatrix}
\leftrightarrow \begin{pmatrix}
+ \\
0 \\
+
\end{pmatrix}
\]
4. Highlights of a Cannibalism & Reproductive Synchrony Model

Veprauskas’ Theorem
Assume there exists a critical trait. Two continua bifurcate at $r_0 = 1$:

- Positive equilibria
- Synchronous 2-cycles

\[
\begin{pmatrix}
\text{juveniles} \\
\text{active adults} \\
\text{inactive adults} \\
\text{trait}
\end{pmatrix}
= \begin{pmatrix} + \\ + \\ + \\ \mathbf{u}_e \end{pmatrix}
\]

Reproductive synchrony
4. Highlights of a Cannibalism & Reproductive Synchrony Model

Veprauskas’ Theorem

There are diagnostic quantities $a_{\pm}$ and $c_w$ such that

<table>
<thead>
<tr>
<th></th>
<th>$a_+ &gt; 0$</th>
<th>$a_+ &lt; 0$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Positive equilibria</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Direction of bifurcation</td>
<td>Backward</td>
<td>Forward</td>
</tr>
<tr>
<td>Stability Properties</td>
<td>Unstable</td>
<td>Stable if $a_- &lt; 0$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unstable if $a_- &gt; 0$</td>
</tr>
<tr>
<td><strong>Synchronous 2-cycles</strong></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Unstable if $a_- &lt; 0$</td>
</tr>
<tr>
<td>( \rho = 0.5 )</td>
<td>( \rho = 0.7 )</td>
<td>( \rho = 0.8 )</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>( r_0 = 0.96, \ R_0 = 0.90 )</td>
<td>( r_0 = 1.09, \ R_0 = 1.26 )</td>
<td>( r_0 = 1.15, \ R_0 = 1.44 )</td>
</tr>
</tbody>
</table>

- Severe degraded environment
- Degraded environment
- Healthy environment

Food resource availability decreases
\( \rho = 0.5 \)
\( r_0 = 0.96, \quad R_0 = 0.90 \)

\( \rho = 0.7 \)
\( r_0 = 1.09, \quad R_0 = 1.26 \)

\( \rho = 0.8 \)
\( r_0 = 1.15, \quad R_0 = 1.44 \)

Evolution selects against & eliminates cannibalism
\[ \rho = 0.5 \quad r_0 = 0.96, \quad R_0 = 0.90 \]

\[ \rho = 0.7 \quad r_0 = 1.09, \quad R_0 = 1.26 \]

\[ \rho = 0.8 \quad r_0 = 1.15, \quad R_0 = 1.44 \]

- Decreased food resource increases cannibalism intensity
- Victim saturation effect promotes reproductive synchrony
\[ \rho = 0.5 \quad r_0 = 0.96, \quad R_0 = 0.90 \]
\[ \rho = 0.7 \quad r_0 = 1.09, \quad R_0 = 1.26 \]
\[ \rho = 0.8 \quad r_0 = 1.15, \quad R_0 = 1.44 \]

Evolution selects for a low level of cannibalism
$\rho = 0.5$
$r_0 = 0.96, \quad R_0 = 0.90$

$\rho = 0.7$
$r_0 = 1.09, \quad R_0 = 1.26$

$\rho = 0.8$
$r_0 = 1.15, \quad R_0 = 1.44$

Diagnostics imply a backward bifurcation

$a_+ = 0.07 > 0$
$c_w = 0.06 > 0$

Initial condition dependent survival
\[ \rho = 0.5 \]
\[ r_0 = 0.96, \quad R_0 = 0.90 \]

\[ \rho = 0.7 \]
\[ r_0 = 1.09, \quad R_0 = 1.26 \]

\[ \rho = 0.8 \]
\[ r_0 = 1.15, \quad R_0 = 1.44 \]
In conclusion ...

1. 2D Juvenile-Adult cannibalism model:
   Cannibalism can “save the day” in degraded environments
In conclusion ...

1. 2D Juvenile-Adult cannibalism model:
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2. Evolutionary (EGT) version of 2D model:
   Evolution can select for cannibalism in degraded environments
In conclusion ...

1. 2D Juvenile-Adult cannibalism model:  
   Cannibalism can “save the day” in degraded environments

2. Evolutionary (EGT) version of 2D model:  
   Evolution can select for cannibalism in degraded environments

3. Periodically forced 2D EGT model:  
   Evolution can select for cannibalism in periodic environments,  
   but against cannibalism in constant or stochastic environments
In conclusion ...

1. 2D Juvenile-Adult cannibalism model:
   Cannibalism can “save the day” in degraded environments

2. Evolutionary (EGT) version of 2D model:
   Evolution can select for cannibalism in degraded environments

3. Periodically forced 2D EGT model:
   Evolution can select for cannibalism is periodic environments, but against cannibalism is constant or stochastic environments

4. Higher dimensional, structured population models to include reproductive synchrony
   Reproductive synchrony occurs as evolution selects for cannibalism in degraded environment
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics
  
  - Cannibalism & reproductive synchrony occur on daily time scale
  - Maturation of juveniles does NOT occur within season, but across seasons
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics

Periodically forced matrix model of the form

\[
P(t, \hat{x}) = \begin{cases} 
W(\hat{x}) & \text{for } t = 0, 1, \ldots, k - 2 \\
A(\hat{x}) & \text{for } t = k - 1 
\end{cases}
\]
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics

Periodically forced matrix model of the form

\[ P(t, \hat{x}) = \begin{cases} W(\hat{x}) & \text{for } t = 0, 1, \ldots, k - 2 \\ A(\hat{x}) & \text{for } t = k - 1 \end{cases} \]

Within-season projection matrix applied \( k - 1 \) times where \( k = \text{season length} \)
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics

Periodically forced matrix model of the form

\[
P(t, \hat{x}) = \begin{cases} W(\hat{x}) & \text{for } t = 0, 1, \ldots, k - 2 \\ A(\hat{x}) & \text{for } t = k - 1 \end{cases}
\]

Across-season projection matrix

Maturation of juveniles occurs across season

\[\begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \end{pmatrix} \rightarrow \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & s_2 \mu & s_3 \mu & s_4 \mu \\ 0 & s_2 (1 - \mu) & s_3 (1 - \mu) & s_4 (1 - \mu) \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \end{pmatrix}\]

A has rank 1.
Most recent project ...

- High dimensional, periodic models to address disparate time scales: within-season versus across-season dynamics

Periodically forced matrix model of the form

\[ P(t, \hat{x}) = \begin{cases} 
W(\hat{x}) & \text{for } t = 0, 1, \ldots, k - 2 \\
A(\hat{x}) & \text{for } t = k - 1
\end{cases} \]

Seasonal composite map can be reduced to a 1D map!

Fundamental Bifurcation Theorem alternatives occur.

Sample Simulation

• Backward bifurcation due to cannibalism.
• Deteriorated environment: $r(0) < 1$.
• Survival (initial condition dependent) as a season cycle.
Sample Simulation

• Backward bifurcation due to cannibalism.
• Deteriorated environment: \( r(0) < 1 \).
• Survival (initial condition dependent) as a season cycle.
• Within-season reproductive synchrony.
Yet to do with the across season model ...

- Study EGT and fluctuating environment versions

  Future projects ...

- Evolution of multiple traits
  
  Theory has been developed for constant environments

- “Super” cannibals (do not gather environment resources)
  
  Cheaters in game theory

- Add predation
  
  Bald eagle predation can be significant in gull colonies
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