The Ecological Effects of Trait Variation in a *u*-Predator, *v*-Prey System

Sam Fleischer, Pablo Chavarria

May 1, 2015

Sigma Xi Student Research Symposium

Advisor:	Dr. Jing Li, Mathematics,	CSU Northridge
Consultant:	Dr. Casey terHorst, Biology,	CSU Northridge
Supported By:	Pacific Math Alliance, PUMP,	CSU Northridge

Overview

- Motivation / Observations in Nature
- Model Formulation
- Preliminary Results
- Future Work

Motivation / Observations in Nature

- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod [Saloniemi, 1993]
  - Protist vs. bacteria [terHorst]
- There is trait variation within species
  - Thickness of plant cuticula [Saloniemi, 1993]
  - Strength of gastropod shell [Saloniemi, 1993]
- Incorporating trait variation provides **richer dynamics** than classical Lotka-Volterra models

Normally Distributed Trait Values

Assume Prey and Predator have normally distributed trait values.

$$p(n,\overline{n}) = \frac{1}{\sqrt{2\pi\beta^2}} \exp\left[-\frac{(n-\overline{n})^2}{2\beta^2}\right]$$

$$p(m,\overline{m}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(m-\overline{m})^2}{2\sigma^2}\right]$$

Variables

- $n \equiv$ Prey Trait Value
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $m \equiv$ Predator Trait Value
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\beta^2 \equiv$ Prey Trait Variance
- $\sigma^2 \equiv$ Predator Trait Variance

Attack Rate as a function of Normally Distributed Trait Values

Attack Rate is a Function of the Prey's Trait Value and the Predator's Trait Value

$$a(n, m) = \alpha \exp\left[-\frac{((m-n)-\theta)^2}{2\tau^2}\right]$$

Variables

- $n \equiv$ Prey Trait Value
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $m \equiv$ Predator Trait Value
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait **difference**
- $\tau^2 \equiv$ Specialization Constant

Attack Rate as a function of Normally Distributed Trait Values

Attack Rate is a Function of the Prey's Trait Value and the Predator's Trait Value

$$a(n, m) = \alpha \exp\left[-\frac{((m-n)-\theta)^2}{2\tau^2}\right]$$

Average Attack Rate

$$\overline{a}(\overline{n}, \overline{m}) = \int_{-\infty}^{\infty}\int_{\infty}^{\infty} a(n, m) \cdot p(n, \overline{n}) \cdot p(m, \overline{m}) \; dn\, dm$$

$$= \frac{\alpha\tau}{\sqrt{\sigma^2+\beta^2+\tau^2}} \exp\left[-\frac{((\overline{m}-\overline{n})-\theta)^2}{2(\sigma^2+\beta^2+\tau^2)}\right]$$

Variables

- $n \equiv$ Prey Trait Value
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $m \equiv$ Predator Trait Value
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait **difference**
- $\tau^2 \equiv$ Specialization Constant
- $\beta^2 \equiv$ Prey Trait Variance
- $\sigma^2 \equiv$ Predator Trait Variance

Intrinsic Growth Rate as a function of the Normally Distributed Trait Value

Prey Growth Rate is is a Function of the Prey's Trait Value

$$r(n) = \rho \exp\left[-\frac{(n-\phi)^2}{2\gamma^2}\right]$$

Parameters

- $\rho \equiv$ Maximum Growth Rate
- $\phi \equiv$ Prey Optimum Trait Value
- $\gamma^2 \equiv$ Stabilizing Selection Constant

Variables

- $n \equiv$ Prey Trait Value
- $\bar{n} \equiv$ **Average** Prey Trait Value

Intrinsic Growth Rate as a function of the Normally Distributed Trait Value

Prey Growth Rate is is a Function of the Prey's Trait Value

$$r(n) = \rho \exp\left[-\frac{(n-\phi)^2}{2\gamma^2}\right]$$

Averge Growth Rate

$$\begin{aligned}\bar{r}(\bar{n}) &= \int_{-\infty}^{\infty} r(n) \cdot p(n, \bar{n}) dn \\ &= \frac{\rho\gamma}{\sqrt{\beta^2+\gamma^2}} \exp\left[-\frac{(n-\phi)^2}{2\gamma^2}\right]\end{aligned}$$

Variables

- $n \equiv$ Prey Trait Value
- $\bar{n} \equiv$ **Average** Prey Trait Value

Parameters

- $\rho \equiv$ Maximum Growth Rate
- $\phi \equiv$ Prey Optimum Trait Value
- $\gamma^2 \equiv$ Stabilizing Selection Constant
- $\beta^2 \equiv$ Prey Trait Variance

Fitness Assumptions

- Prey experiences logistic growth in absence of predator
- Predator experiences exponential decay in absence of prey

$$Y(N, n, M, m) = r(n)\left(1 - \frac{N}{K}\right) - Ma(n, m)$$

$$W(N, n, M, m) = eNa(n, m) - d$$

Variables

- $N \equiv$ Prey Density
- $n \equiv$ Prey Trait Value
- $M \equiv$ Predator Density
- $m \equiv$ Predator Trait Value

Parameters

- $r \equiv$ Intrinsic Prey Growth Rate Function
- $K \equiv$ Prey Carrying Capacity
- $d \equiv$ Predator Death Rate
- $e \equiv$ Efficiency

Average Fitness

$$\overline{Y}(N,\overline{n},M,\overline{m}) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} Y(N,n,M,m)\cdot p(m,\overline{m})\cdot p(n,\overline{n})\ dmdn$$
$$= \overline{r}(\overline{n})\left(1-\frac{N}{K}\right) - M\overline{a}(\overline{n},\overline{m})$$

$$\overline{W}(N,\overline{n},M,\overline{m}) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} W(N,n,M,m)\cdot p(m,\overline{m})\cdot p(n,\overline{n})\ dmdn$$
$$= eN\overline{a}(\overline{n},\overline{m}) - d$$

Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\overline{r} \equiv$ Average Intrinsic Prey Growth Rate Function
- $K \equiv$ Prey Carrying Capacity
- $d \equiv$ Predator Death Rate
- $e \equiv$ Efficiency

Ecological Components

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) = N\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right) - M\overline{a}(\overline{n}, \overline{m})\right]$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) = M[eN\overline{a}(\overline{n}, \overline{m}) - d]$$

$$\xrightarrow{\overline{r}(\overline{n})N(1-\frac{N}{K})} N \xrightarrow{\overline{a}(\overline{n},\overline{m})MN} \quad \xrightarrow{e\overline{a}(\overline{n},\overline{m})MN} M \xrightarrow{dM}$$

Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\overline{r} \equiv$ Average Intrinsic Prey Growth Rate Function
- $K \equiv$ Prey Carrying Capacity
- $d \equiv$ Predator Death Rate
- $e \equiv$ Efficiency

Evolutionary Components

- The evolution of the average trait value is always in the direction which increases the mean fitness in the population. [Lande, 1976]

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \left[\overline{r}(\overline{n}) \left(1 - \frac{N}{K} \right) \frac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \frac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n}) \right]$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta + \overline{n} - \overline{m})}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n})$$

Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ **Average** Prey Trait Value
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ **Average** Predator Trait Value

Parameters

- $\phi \equiv$ Prey Optimum Trait Value
- $\gamma^2 \equiv$ Stabilizing Selection Constant
- $\overline{r} \equiv$ Average Intrinsic Prey Growth Rate Function
- $\beta_G^2 \equiv$ Prey genetic variance
- $\sigma_G^2 \equiv$ Predator genetic variance

The Complete 1 × 1 Model (One Predator Species, One Prey Species)

Ecological Components

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) = N\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right) - M\overline{a}(\overline{n}, \overline{m})\right]$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) = M[eN\overline{a}(\overline{n}, \overline{m}) - d]$$

Evolutionary Components

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right)\frac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \frac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2}\overline{a}(\overline{m}, \overline{n})\right]$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta + \overline{n} - \overline{m})}{\sigma^2 + \beta^2 + \tau^2}\overline{a}(\overline{m}, \overline{n})$$

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

Exclusion

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \_, \_)$$

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{\textit{Unstable}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

Exclusion

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \_, \_)$$

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{\textit{Unstable}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

Exclusion $\boxed{\textit{Locally stable under certain conditions}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \_, \_)$$

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{\textit{Unstable}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

Exclusion $\boxed{\textit{Locally stable under certain conditions}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \_, \_)$$

Necessary Conditions for Locally Stable Exclusion:

- $d > e\overline{a}(\overline{m}^*, \overline{n}^*)K$
- $(\overline{m}^* - \overline{n}^* - \theta)^2 < \sigma^2 + \beta^2 + \tau^2$

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Coexistence

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \Big(\frac{d\sqrt{A}}{e\alpha\tau} \; , \; \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right) \; , \; \theta \; , \; \theta + \phi\Big)$$

where $A = \sigma^2 + \beta^2 + \tau^2$ and $B = \beta^2 + \gamma^2$

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Coexistence $\boxed{\textit{Locally stable under certain conditions}}$

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}\ ,\ \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)\ ,\ \theta\ ,\ \theta + \phi\right)$$

where $A = \sigma^2 + \beta^2 + \tau^2$ and $B = \beta^2 + \gamma^2$

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Coexistence $\boxed{\textit{Locally stable under certain conditions}}$

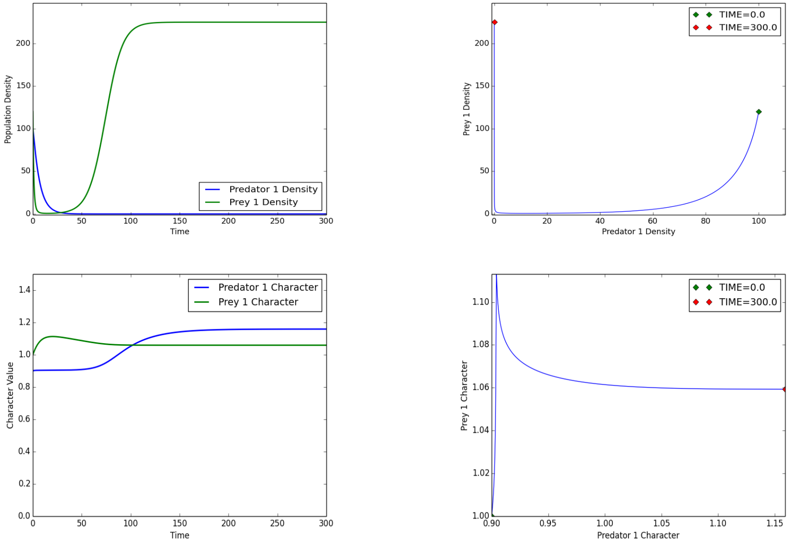
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau} \, , \, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right) \, , \, \theta \, , \, \theta + \phi\right)$$

where $A = \sigma^2 + \beta^2 + \tau^2$ and $B = \beta^2 + \gamma^2$

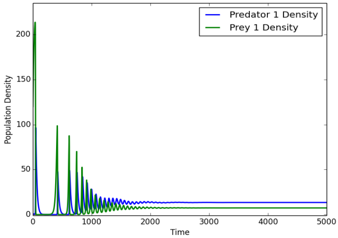
Necessary Condition for Locally Stable Coexistence:

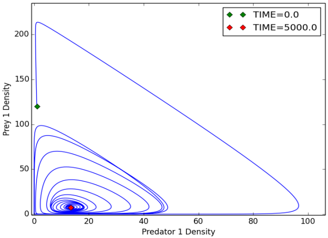
- $$\frac{\sigma_G^2}{\beta_G^2} > \frac{\rho\gamma}{d\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)\left(1 - \frac{A}{B}\right)$$

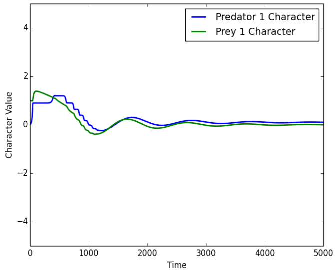
Figures - 1 × 1 - Stable Exclusion

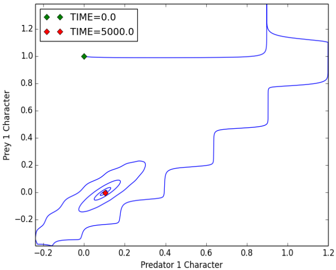


Figures - 1×1 - Stable Coexistence

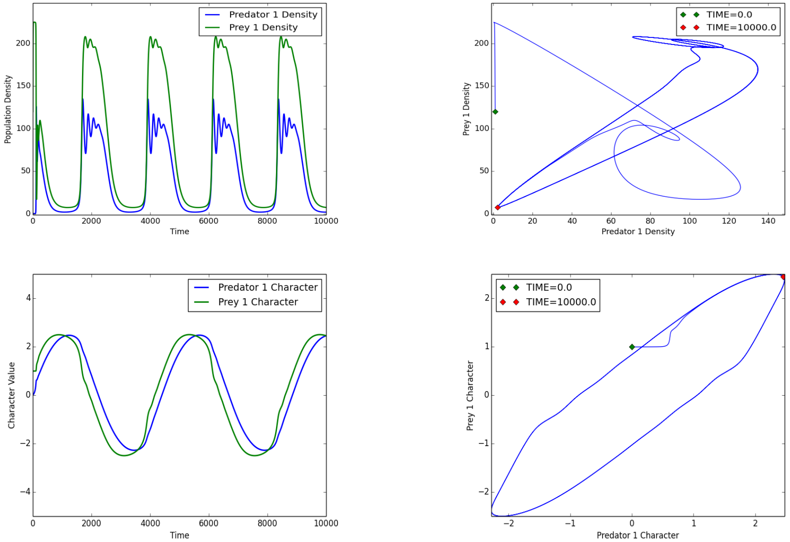








Figures - 1×1 - Stable Cycles (Red Queen Dynamics)[Kindrik, Kondrashov, 1994]



Prey Fitness

$$Y(N,n,M,m) = r(n)\left(1-\frac{N}{K}\right) - Ma(n,m)$$

Predator Fitness

$$W(N,n,M,m) = eNa(n,m) - d$$

Prey Fitness

$$Y(N,n,M,m) = r(n)\left(1 - \frac{N}{K}\right) - Ma(n,m)$$

$$\downarrow$$

$$Y_j(N_j, n_j, [M_i]_{i=1}^u, [m_i]_{i=1}^u) = r_j(n_j)\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} M_i a_{ij}(n_j, m_i)$$

Predator Fitness

$$W(N,n,M,m) = eNa(n,m) - d$$

Notation

$$[x_i]_{i=1}^u = x_1, \ldots, x_u$$

Prey Fitness

$$Y(N, n, M, m) = r(n)\left(1 - \frac{N}{K}\right) - Ma(n, m)$$

$$\downarrow$$

$$Y_j(N_j, n_j, [M_i]_{i=1}^u, [m_i]_{i=1}^u) = r_j(n_j)\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} M_i a_{ij}(n_j, m_i)$$

Predator Fitness

$$W(N, n, M, m) = eNa(n, m) - d$$

$$\downarrow$$

$$W_i([N_j]_{j=1}^v, [n_j]_{j=1}^v, M_i, m_i) = \sum_{j=1}^{v}\left[e_{ij} N_j a_{ij}(n_j, m_i)\right] - d_i$$

Notation

$$[x_i]_{i=1}^u = x_1, \ldots, x_u$$

,

Average Fitness

$$\overline{Y}_j(N_j, \overline{n_j}, [M_i]_{i=1}^u, [\overline{m_i}]_{i=1}^u)$$

$$= \int\limits_{\mathbb{R}^{u+1}} Y_j \cdot \prod_{i=1}^{u} \left[p_i(m_i, \overline{m_i}) \right] \cdot p(n, \overline{n}) \prod_{i=1}^{u} \left[dm_i \right] dn_j$$

$$= \overline{r_j}(\overline{n_j}) \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^{u} M_i \overline{a}_{ij}(\overline{n}_j, \overline{m}_i)$$

$$\overline{W}_i(N_j, \overline{n_j}, [M_i]_{i=1}^u, [\overline{m_i}]_{i=1}^u)$$

$$= \int\limits_{\mathbb{R}^{u+1}} W_i \cdot p_i(m_i, \overline{m_i}) \cdot \prod_{j=1}^{v} \left[p(n_j, \overline{n}_j) \right] dm_i \prod_{j=1}^{v} \left[dn_j \right]$$

$$= \sum_{j=1}^{v} \left[e_{ij} N_j \overline{a}_{ij}(\overline{n}_j, \overline{m}_i) \right] - d_i$$

The Complete $u \times v$ Model (u Predator Species, v Prey Species)

Ecological Components

$$\frac{dN_j}{dt} = N_j \overline{Y}_j = N_j \left[\overline{r_j}(\overline{n_j}) \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} M_i \bar{a}_{ij}(\overline{n}_j, \overline{m}_i) \right]$$

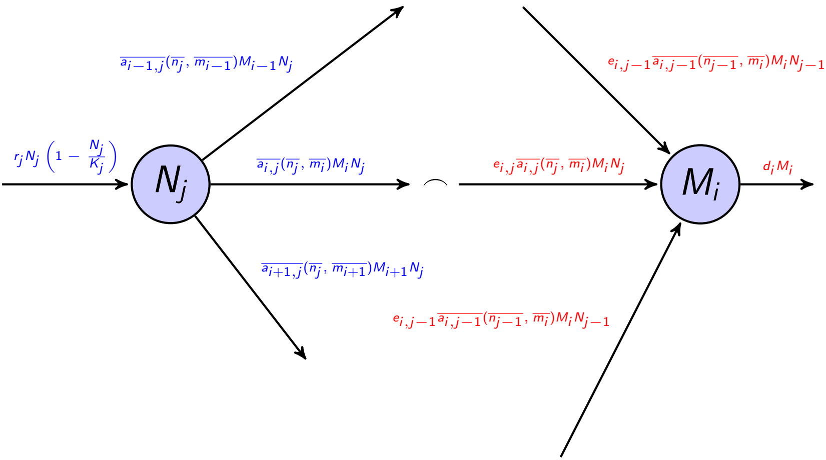
$$\frac{dM_i}{dt} = M_i \overline{W}_i = M_i \left[\sum_{j=1}^{v} \left[e_{ij} N_j \bar{a}_{ij}(\overline{m}_i, \overline{n}_j) \right] - d_i \right]$$

Evolutionary Components

$$\frac{d\overline{n}_j}{dt} = \beta_{Gj}^2 \frac{\partial \overline{Y}_j}{\partial \overline{n}_j} = \beta_{Gj}^2 \sum_{i=1}^{u} \left[\frac{M_i(\theta_{ij} + \overline{n_j} - \overline{m_i})}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \overline{a}_{ij}(\overline{m_i}, \overline{n_j}) \right]$$

$$\frac{d\overline{m}_i}{dt} = \sigma_{Gi}^2 \frac{\partial \overline{W}_i}{\partial \overline{m}_i} = \sigma_{Gi}^2 \sum_{j=1}^{v} \left[\frac{e_{ij} N_j(\theta_{ij} + \overline{n_j} - \overline{m_i})}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \overline{a}_{ij}(\overline{m_i}, \overline{n_j}) \right]$$

The Complete $u \times v$ Model (u Predator Species, v Prey Species)



Future Work

- Two Predators competing for One Prey
- One Specialist Predator Competing with One Generalist Predator for Two Prey Species
- Two Specialist Predators Competing with One Generalist Predator for Two Prey Species
- Further Analysis of the General $u \times v$ Model
- Intra-Guild Predation
- Adding Evolutionary Cost to Prey
- Adding Evolutionary Cost to Predator

Thank You!

- Pacific Coast Undergraduate Math Conference
- Dr. Alissa Crans, Dr. Karrolyne Fogel, Dr. Kendra Killpatrick, Dr. John Rock, and all other PCUMC Organizers
- National Science Foundation
- Mathematical Association of America and all other PCUMC sponsors
- Cal Lutheran University and all other PCUMC university supporters
- Dr. Helena Noronha
- Pacific Math Alliance PUMP Undergraduate Research Groups
- California State University, Northridge
- Dr. Jing Li and Dr. Casey terHorst

Questions?

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \_, \_, \_)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{Unstable}$

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \_, \_, \_)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta^2_{G1} \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta^2_{G2} \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma^2_G \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{\textit{Unstable}}$

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \_, \_, \_)$$

Exclusion

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (K_1, K_2, 0, \_, \_, \_)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction $\boxed{\textit{Unstable}}$

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \_, \_, \_)$$

Exclusion $\boxed{\textit{Stable under certain conditions}}$

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (K_1, K_2, 0, \_, \_, \_)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Generalist Becomes Specialist

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*)$$
$$= \Big(\frac{d\sqrt{A_1}}{e_1\alpha_1\tau_1}\ ,\ K_2\ ,\ \frac{r_1\sqrt{A_1}}{\alpha_1\tau_1}\left(1 - \frac{d\sqrt{A_1}}{K_1 e_1\alpha_1\tau_1}\right)\ ,\ \mu_1^*\ ,\ \mu_2^*\ ,\ \mu_1^* - \theta_1\Big)$$

where $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$, μ_1^* is an arbitrary value, and μ_2^* is sufficiently far from $\mu_1^* - \theta_1$.

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Generalist Becomes Specialist $\boxed{\textit{Stable under certain conditions???}}$

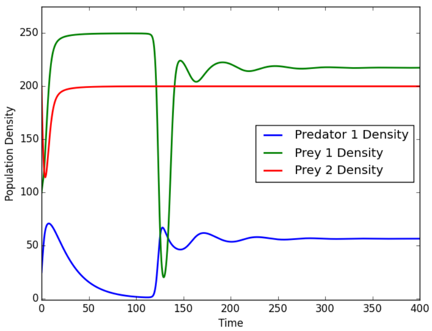
$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*)$$

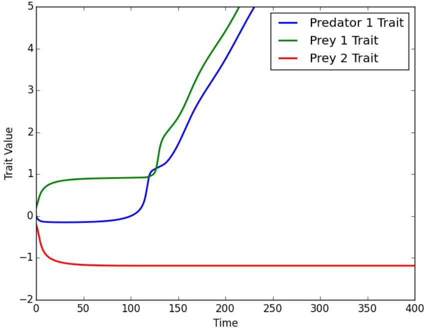
$$= \left(\frac{d\sqrt{A_1}}{e_1 \alpha_1 \tau_1} \ , \ K_2 \ , \ \frac{r_1 \sqrt{A_1}}{\alpha_1 \tau_1} \left(1 - \frac{d\sqrt{A_1}}{K_1 e_1 \alpha_1 \tau_1} \right) \ , \ \mu_1^* \ , \ \mu_2^* \ , \ \mu_1^* - \theta_1 \right)$$

where $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$, μ_1^* is an arbitrary value, and μ_2^* is sufficiently far from $\mu_1^* - \theta_1$.

Figures - 1×2

Generalist Becomes Specialist





Figures - 1×2

Unstable Coexistence