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

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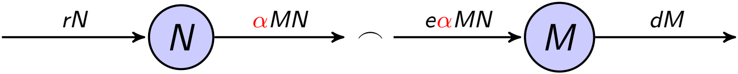
Overview

- Motivation / Observations in Nature
- Model Formulation
  - Classical Lotka-Volterra Predator-Prey Model
  - Schreiber, Bürger, and Bolnick's Extension
  - Our Extension
- Preliminary Results
- Future Work

Motivation / Observations in Nature

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

Classical Lotka-Volterra Model



$$\frac{dN}{dt} = N(r - \alpha M)$$

$$\frac{dM}{dt} = M(e\alpha N - d)$$

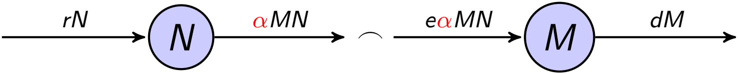
Variables

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density

Parameters

- $\alpha \equiv$ Attack rate
- $r \equiv$ Prey birth rate
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

Classical Lotka-Volterra Model



$$\frac{dN}{dt} = N(r - \alpha M)$$
$$\frac{dM}{dt} = M(e\alpha N - d)$$

Variables

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density

Parameters

- $\alpha \equiv$ Attack rate $\longleftarrow$ **No variation!**
- $r \equiv$ Prey birth rate
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

Schreiber, Bürger, and Bolnick's Extension

Assume the Predator Species has a normally distributed trait value.

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

Variables

- $m \equiv$ Predator Trait Value

Parameters

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

Schreiber, Bürger, and Bolnick's Extension

Assume the Predator Species has a normally distributed trait value.

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

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

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

Variables

- $m \equiv$ Predator Trait Value

Parameters

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

Schreiber, Bürger, and Bolnick's Extension

Assume the Predator Species has a normally distributed trait value.

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

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

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

Variables

- $m \equiv$ Predator Trait Value
- (((No Prey Character)))

Parameters

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

  ↑ **No variation!**

Our Extension

Assume Prey and Predator have normally distributed trait values.

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

Variables

- $n \equiv$ Prey Trait Value
- $m \equiv$ Predator Trait Value

Parameters

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

Our Extension

Assume Prey and Predator have normally distributed trait values.

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

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
- $m \equiv$ Predator Trait Value

Parameters

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

Average Attack Rate

$$\overline{a}(\overline{n}, \overline{m}) = \int_{-\infty}^{\infty} \int_{\infty}^{\infty} a(n, m) \cdot p(n, \overline{n}) \cdot p(m, \overline{m}) \; d n d m$$
$$= \frac{\alpha\tau}{\sqrt{\sigma^2 + \beta^2 + \tau^2}} \exp\left[-\frac{((\overline{m} - \overline{n}) - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)} \right]$$

Variables

- $\overline{n} \equiv$ Mean Prey Character
- $\overline{m} \equiv$ Mean Predator Character

Parameters

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

Fitness Assumptions

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

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

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
- $K \equiv$ Prey Carrying Capacity
- $d \equiv$ Predator Death Rate
- $e \equiv$ Efficiency

Average Fitness

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

Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ Mean Prey Character
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ Mean Predator Character

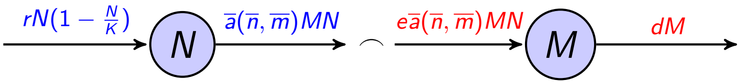
Parameters

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

Ecological Components

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

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



Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ Mean Prey Character
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ Mean Predator Character

Parameters

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

Evolutionary Components

- The evolution of the mean character is always in the direction which increases the mean fitness in the population.

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

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

Variables

- $N \equiv$ Prey Density
- $\overline{n} \equiv$ Mean Prey Character
- $M \equiv$ Predator Density
- $\overline{m} \equiv$ Mean Predator Character

Parameters

- $\beta_G^2 \equiv$ Prey genetic variance
- $\sigma_G^2 \equiv$ Predator genetic variance

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

Ecological Components

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

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

Evolutionary Components

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

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

Equilibria - 1 × 1

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

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

Extinction

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

Exclusion

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

Equilibria - 1×1

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

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

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

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

Exclusion

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

Equilibria - 1×1

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

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

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

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

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

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

Equilibria - 1×1

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

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

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

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

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

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

Necessary Conditions for 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

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

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

Coexistence

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

where $A = \sigma^2 + \beta^2 + \tau^2$ and μ^* is an arbitrary value.

Equilibria - 1×1

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

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

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

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

where $A = \sigma^2 + \beta^2 + \tau^2$ and μ^* is an arbitrary value.

Equilibria - 1 × 1

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

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

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

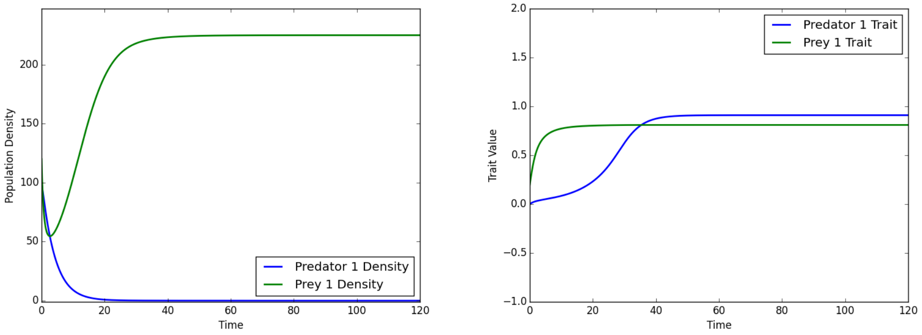
where $A = \sigma^2 + \beta^2 + \tau^2$ and μ^* is an arbitrary value.

Necessary Condition for Stable Coexistence:

- $d\sigma_G^2 > r\beta_G^2 \left(1 - \dfrac{d\sqrt{A}}{Ke\alpha\tau}\right)$

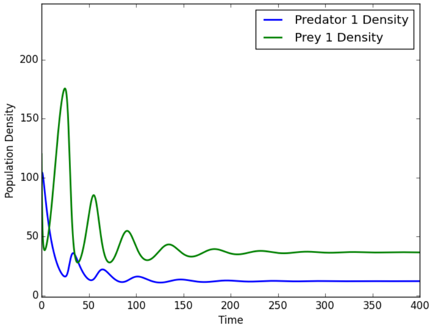
Figures - 1×1

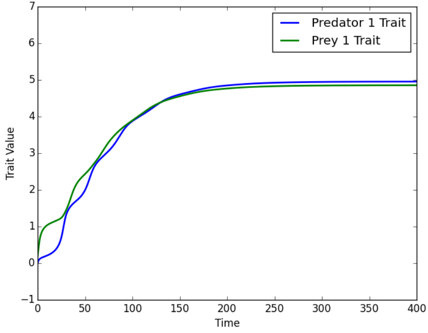
Exclusion



Figures - 1×1

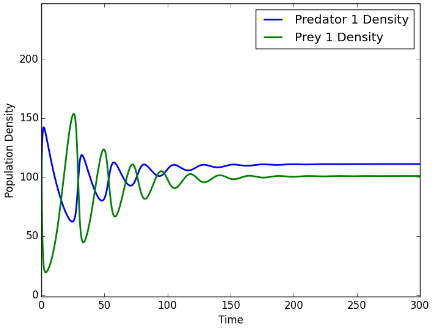
Stable Coexistence

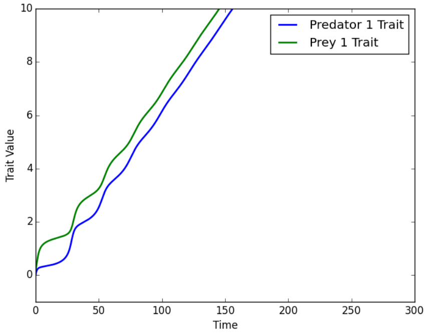




Figures - 1×1

Unstable Coexistence





Ask us about our preliminary 1×2 results!

Prey Fitness

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

Predator Fitness

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

Prey Fitness

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

$$\downarrow$$

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

Predator Fitness

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

Notation

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

Prey Fitness

$$Y(m, n, M, N) = r\left(1 - \frac{N}{K}\right) - Ma(n, m)$$
$$\downarrow$$
$$Y_j([m_i]_{i=1}^{u}, n_j, [M_i]_{i=1}^{u}, N_j) = r_j\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} M_i a_{ij}(n_j, m_i)$$

Predator Fitness

$$W(m, n, N) = eNa(n, m) - d$$
$$\downarrow$$
$$W_i(m_i, [n_j]_{j=1}^{v}, [N_j]_{j=1}^{v}) = \sum_{j=1}^{v}\left[e_{ij} N_j a_{ij}(n_j, m_i)\right] - d_i$$

Notation

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

Average Fitness

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

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

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

$$\overline{W}_i(\overline{m}_i, [\overline{n}_j]_{j=1}^v, [N_j]_{j=1}^v)$$

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

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

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

Ecological Components

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

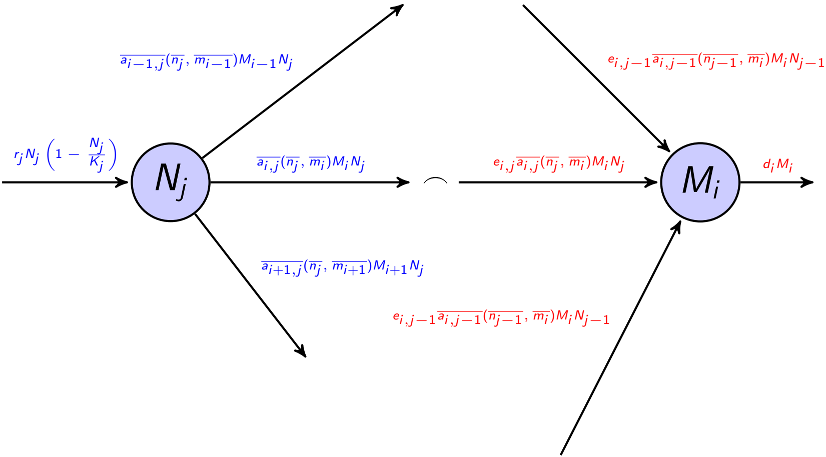
$$\frac{dM_i}{dt} = M_i \overline{W}_i = M_i \left[\sum_{j=1}^{v} \left[e_{ij} N_j \bar{a}_{ij}(\overline{m}_i, \overline{n}_j) \right] - d_i \right]$$

Evolutionary Components

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

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

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
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- 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 $\boxed{\textit{Unstable}}$

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

Equilibria - 1×2

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

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

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

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

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

Exclusion

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

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

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

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

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

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

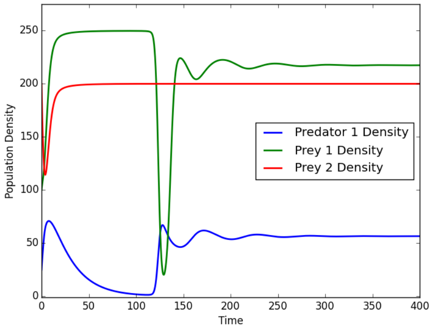
$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*)$$

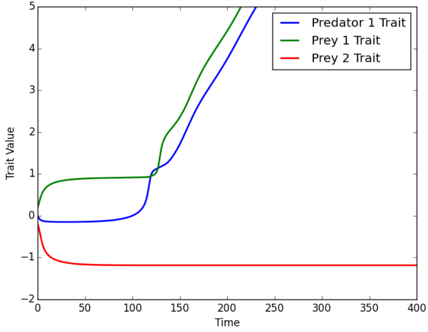
$$= \left(\frac{d\sqrt{A_1}}{e_1 \alpha_1 \tau_1} \,,\; K_2 \,,\; \frac{r_1\sqrt{A_1}}{\alpha_1 \tau_1}\left(1 - \frac{d\sqrt{A_1}}{K_1 e_1 \alpha_1 \tau_1}\right) \,,\; \mu_1^* \,,\; \mu_2^* \,,\; \mu_1^* - \theta_1\right)$$

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