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Thank You

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

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Introduction

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## **Observations**

- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod
  - Protist vs. bacteria
- There is trait variation within species
  - Thickness of plant cuticula
  - Strength of gastropod shell
- 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**

- $N \equiv \text{Prey Density}$
- $M \equiv \text{Predator Density}$

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



# Classical Lotka-Volterra Model



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

#### **Variables**

- N ≡ Prey Density
- $M \equiv \text{Predator Density}$

- $\alpha \equiv$  Attack rate  $\leftarrow$  *No variation!*
- $r \equiv \text{Prey birth rate}$
- $e \equiv \text{Efficiency}$
- $d \equiv \text{Predator death rate}$



# Schreiber, Bürger, and Bolnick's Extension

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

## **Variables**

- $N \equiv \text{Prey Density}$
- $M \equiv \text{Predator Density}$
- $m \equiv \text{Predator Character (Trait Value)}$

- $\alpha \equiv \text{Maximum attack rate}$
- $\theta \equiv Optimal trait value$
- $\tau \equiv$  Specialization Constant

# Schreiber, Bürger, and Bolnick's Extension

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

## **Variables**

- $N \equiv \text{Prey Density}$
- $M \equiv \text{Predator Density}$
- No Prey Character
- $m \equiv \text{Predator Character (Trait Value)}$

- $\alpha \equiv \text{Maximum attack rate}$
- $\theta \equiv \text{Optimal trait value} \quad \longleftarrow \text{No variation!}$
- $oldsymbol{ au} au \equiv {\sf Specialization} \ {\sf Constant}$

# Our Extension

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

## **Variables**

- $N \equiv \text{Prey Density}$
- $M \equiv \text{Predator Density}$
- $n \equiv \text{Prey Character (Trait Value)}$
- $m \equiv \text{Predator Character (Trait Value)}$

- $\alpha \equiv \text{Maximum attack rate}$
- $\theta \equiv \text{Optimal trait } \frac{\text{difference}}{\text{difference}}$
- $oldsymbol{ au} au \equiv {\sf Specialization} \ {\sf Constant}$

## **Distribution Assumptions**

Trait values are normally distributed over the populations

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

## **Variables**

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

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

# Average Attack Rate

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

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

#### **Variables**

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

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

# Fitness Assumptions

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

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

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

#### **Variables**

- $N \equiv \text{Prey Density}$
- $n \equiv \text{Prey Character}$
- $M \equiv \text{Predator Density}$
- m ≡ Predator Character

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

## Average Fitness

$$\overline{Y}(\overline{m}, \overline{n}, M, N) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} Y(m, n, M, N) \cdot p(m, \overline{m}) \cdot p(n, \overline{n}) dm dn$$

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

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

$$= eN \overline{a}(\overline{m}, \overline{n}) - d$$

## **Variables**

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

- $r \equiv$  Intrinsic Prey Growth Rate
- $K \equiv \text{Prey Carrying Capacity}$



# **Ecological Components**

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

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

#### **Variables**

- N ≡ Prey Density
- $\overline{n} \equiv$  Mean Prey Character
- $M \equiv \text{Predator Density}$
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- $r \equiv$  Intrinsic Prey Growth Rate
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- $e \equiv \text{Efficiency}$



## **Evolutionary Components**

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

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

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

#### **Variables**

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

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

# The Complete $1 \times 1$ Model (One Predator Species, One Prey Species)

## **Ecological Components**

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

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

## **Evolutionary Components**

$$\begin{split} \frac{d\overline{n}}{dt} &= \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \frac{M(\theta + \overline{n} - \overline{m})}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n}) \\ \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta + \overline{n} - \overline{m})}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n}) \end{split}$$

# **Prey Fitness**

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

#### **Predator Fitness**

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

## **Prey Fitness**

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

$$\downarrow$$

$$r \left(1 - \frac{N_j}{K}\right) = \sum_{i=1}^{n} Ma_i(m, n)$$

$$Y_{j}([m_{i}]_{i=1}^{u}, n_{j}, [M_{i}]_{i=1}^{u}, N_{j}) = r_{j} \left(1 - \frac{N_{j}}{K_{j}}\right) - \sum_{i=1}^{u} M_{i} a_{ij}(m_{i}, n_{j})$$

### **Predator Fitness**

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

#### **Notation**

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

## **Prey Fitness**

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

$$\downarrow$$

$$Y_{j}([m_{i}]_{i=1}^{u}, n_{j}, [M_{i}]_{i=1}^{u}, N_{j}) = r_{j} \left(1 - \frac{N_{j}}{K_{j}}\right) - \sum_{i=1}^{u} M_{i} a_{ij}(m_{i}, n_{j})$$

#### **Predator Fitness**

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

$$\downarrow$$

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

#### Notation

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

## **Average Fitness**

$$\begin{split} \overline{Y}_{j}([\overline{m}_{i}]_{i=1}^{u}, \overline{n}_{j}, [M_{i}]_{i=1}^{u}, N_{j}) \\ &= \int_{\mathbb{R}^{u+1}} Y_{j} \cdot \prod_{i=1}^{u} \left[ p_{i}(m_{i}, \overline{m_{i}}) \right] \cdot p(n, \overline{n}) \prod_{i=1}^{u} \left[ dm_{i} \right] dn_{j} \\ &= r_{j} \left( 1 - \frac{N_{j}}{K_{j}} \right) - \sum_{i=1}^{u} M_{i} \overline{a}_{ij}(\overline{m}_{i}, \overline{n}_{j}) \end{split}$$

$$\begin{split} \overline{W}_{i}(\overline{m}_{i}, [\overline{n}_{j}]_{j=1}^{\nu}, [N_{j}]_{j=1}^{\nu}) \\ &= \int_{\mathbb{R}^{u+1}} W_{i} \cdot p_{i}(m_{i}, \overline{m_{i}}) \cdot \prod_{j=1}^{v} \left[ p(n_{j}, \overline{n}_{j}) \right] dm_{i} \prod_{j=1}^{v} \left[ dn_{j} \right] \\ &= \sum_{j=1}^{v} \left[ e_{ij} N_{j} \overline{a}_{ij}(\overline{m}_{i}, \overline{n}_{j}) \right] - d_{i} \end{split}$$

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

## **Ecological Components**

$$\frac{dN_{j}}{dt} = N_{j}\overline{Y}_{j} = N_{j} \left[ r_{j} \left( 1 - \frac{N_{j}}{K_{j}} \right) - \sum_{i=1}^{u} M_{i}\overline{a}_{ij}(\overline{m}_{i}, \overline{n}_{j}) \right]$$

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

# **Evolutionary Components**

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

$$\frac{d\overline{m}_{i}}{dt} = \sigma_{Gi}^{2} \frac{\partial \overline{W}_{i}}{\partial \overline{m}_{i}} = \sigma_{Gi}^{2} \sum_{i=1}^{v} \left[ \frac{e_{ij} N_{j} (\theta_{ij} + \overline{n_{j}} - \overline{m_{i}})}{\sigma_{i}^{2} + \beta_{j}^{2} + \tau_{ij}^{2}} \overline{a}_{ij} (\overline{m_{i}}, \overline{n_{j}}) \right]$$

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

#### Extinction

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

#### **Exclusion**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \underline{\hspace{1em}}, \underline{\hspace{1em}})$$

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

# **Extinction** *Unstable*

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

#### **Exclusion**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \underline{\hspace{1em}}, \underline{\hspace{1em}})$$

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**Extinction** *Unstable* 

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

**Exclusion** | Stable under certain conditions

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\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** *Unstable* 

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

**Exclusion** | Stable under certain conditions

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

## **Necessary Conditions for Stable Exclusion:**

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

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

#### 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  $\mu^*$  is an arbitrary value.

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

# **Coexistence** Stable under certain conditions

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (\frac{d\sqrt{A}}{e\alpha\tau}, \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \mu^*, \mu^* - \theta)$$
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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Coexistence** Stable under certain conditions

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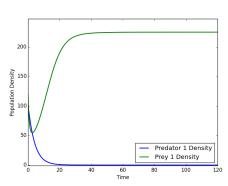
where  $A = \sigma^2 + \beta^2 + \tau^2$  and  $\mu^*$  is an arbitrary value.

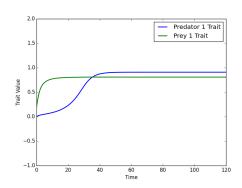
# **Necessary Condition for Stable Coexistence:**

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

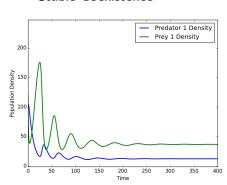


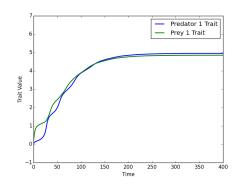
## **Exclusion**



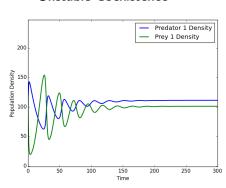


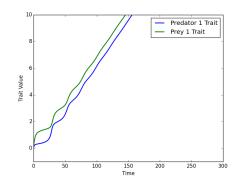
## **Stable Coexistence**





#### **Unstable Coexistence**





$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial Y_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

## **Extinction**

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

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

# **Extinction** *Unstable*

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

$$\begin{split} \frac{dN_1}{dt} &= N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) & \frac{d\overline{n}_1}{dt} &= \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\ \frac{dN_2}{dt} &= N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) & \frac{d\overline{n}_2}{dt} &= \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\ \frac{dM}{dt} &= M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) & \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} \end{split}$$

# **Extinction** *Unstable*

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

#### **Exclusion**

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

$$\begin{split} \frac{dN_1}{dt} &= N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) & \frac{d\overline{n}_1}{dt} &= \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\ \frac{dN_2}{dt} &= N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) & \frac{d\overline{n}_2}{dt} &= \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\ \frac{dM}{dt} &= M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) & \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} \end{split}$$

**Extinction** *Unstable* 

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

**Exclusion** Stable under certain conditions

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

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial Y_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

# **Generalist Becomes Specialist**

$$\begin{array}{l} \left(N_{1}^{*} \quad , \; N_{2}^{*} \; , \; M^{*} \qquad \qquad , \; \overline{n}_{1}^{*} \; , \; \overline{n}_{2}^{*} \; , \; \overline{m}^{*} \quad \right) \\ \\ = \left(\frac{d\sqrt{A_{1}}}{e_{1}\alpha_{1}\tau_{1}} \; , \; K_{2} \; , \; \frac{r_{1}\sqrt{A_{1}}}{\alpha_{1}\tau_{1}} \left(1 - \frac{d\sqrt{A_{1}}}{K_{1}e_{1}\alpha_{1}\tau_{1}}\right) \; , \; \mu_{1}^{*} \; , \; \mu_{2}^{*} \; , \; \mu_{1}^{*} - \theta_{1}\right) \\ \end{array}$$

where  $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$ ,  $\mu_1^*$  is an arbitrary value, and  $\mu_2^*$  is sufficiently far from  $\mu_1^* - \theta_1$ .

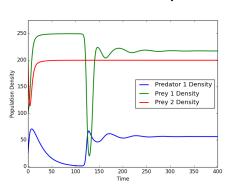
$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

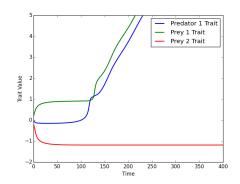
Generalist Becomes Specialist | Stable under certain conditions???

$$\begin{array}{l} \left(\textit{N}_{1}^{*} \ , \ \textit{N}_{2}^{*} \ , \ \textit{M}^{*} \right. \\ \\ = \left(\frac{d\sqrt{\textit{A}_{1}}}{\textit{e}_{1}\alpha_{1}\tau_{1}} \ , \ \textit{K}_{2} \ , \ \frac{\textit{r}_{1}\sqrt{\textit{A}_{1}}}{\alpha_{1}\tau_{1}} \left(1 - \frac{d\sqrt{\textit{A}_{1}}}{\textit{K}_{1}\textit{e}_{1}\alpha_{1}\tau_{1}}\right) \ , \ \mu_{1}^{*} \ , \ \mu_{2}^{*} \ , \ \mu_{1}^{*} - \theta_{1}\right) \\ \end{array}$$

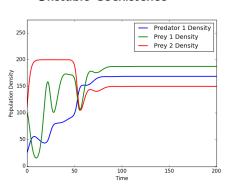
where  $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$ ,  $\mu_1^*$  is an arbitrary value, and  $\mu_2^*$  is sufficiently far from  $\mu_1^* - \theta_1$ .

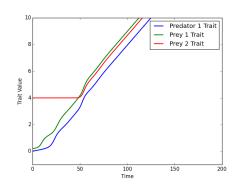
## **Generalist Becomes Specialist**





## **Unstable Coexistence**





- 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!

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Introduction Motivation Model Formulation Preliminary Results Possible Expansions Thank You

# Questions?