

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

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Supported By: Pacific Math Alliance, PUMP, CSU Northridge

Overview

- Motivation
- Proposed Model
- Results / Discussion

Observations in Nature

- Predator/Prey interactions are prevalent in nature
 - Crab vs. gastropod [Saloniemi, 1993]
 - Classical Lotka-Volterra model (Next Slide)

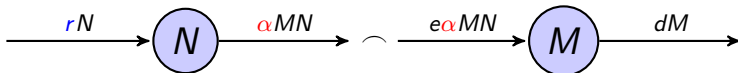


Observations in Nature

- Predator/Prey interactions are prevalent in nature
 - Crab vs. gastropod [Saloniemi, 1993]
 - Classical Lotka-Volterra model (Next Slide)
- There is trait variation within species, which causes **variation in fundamental model parameters**
 - Relative strength of crab claw vs. gastropod shell [Saloniemi, 1993]
 - Incorporating trait variation provides **richer dynamics** than classical Lotka-Volterra models



Classical Lotka-Volterra Model



Variables

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

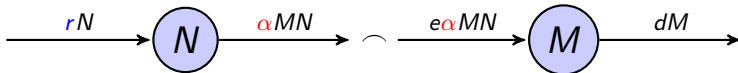
Parameters

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

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

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

Classical Lotka-Volterra Model



Variables

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

Parameters

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

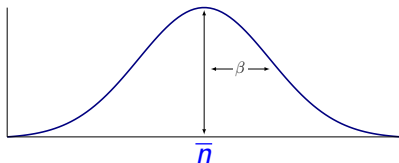
$$\frac{dN}{dt} = N(r - \alpha M)$$

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

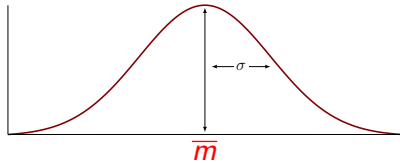
Normally Distributed Trait Values

Assume **Prey** and **Predator** have normally distributed trait values.

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



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



Variables

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

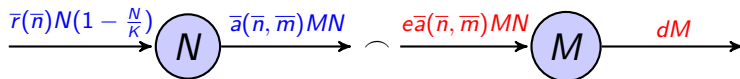
Parameters

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

Ecological Components

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

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



Variables

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

Parameters

- $\bar{a} \equiv$ Average Attack Rate **Function**
- $\bar{r} \equiv$ 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]

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \bar{Y}}{\partial \bar{n}} = \beta_G^2 \left[\frac{d\bar{r}}{d\bar{n}} \left(1 - \frac{N}{K} \right) - M \frac{\partial \bar{a}}{\partial \bar{n}} \right]$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}} = \sigma_G^2 \left[eN \frac{\partial \bar{a}}{\partial \bar{m}} \right]$$

Variables

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

Parameters

- $\bar{a} \equiv$ Average Attack Rate Function
- $\bar{r} \equiv$ Average Intrinsic Prey Growth Rate Function
- $\beta_G^2 \equiv$ Prey genetic variance
- $\sigma_G^2 \equiv$ Predator genetic variance

Our Proposed 1×1 Model (One Prey Species, One Predator Species)

Ecological Components

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

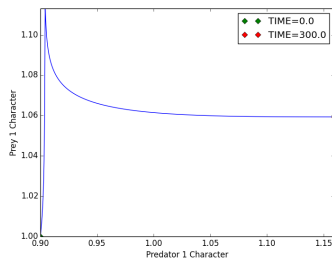
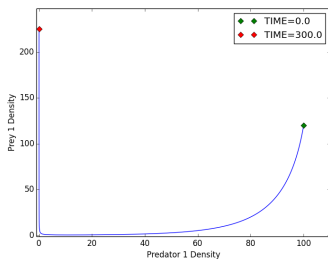
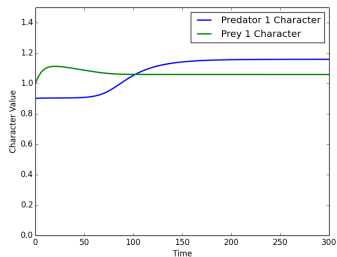
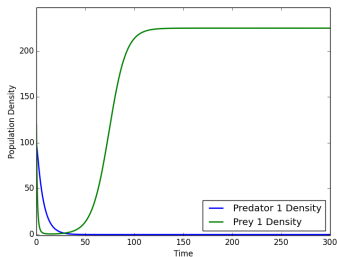
$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m}) = M [eN \bar{a}(\bar{n}, \bar{m}) - d]$$

Evolutionary Components

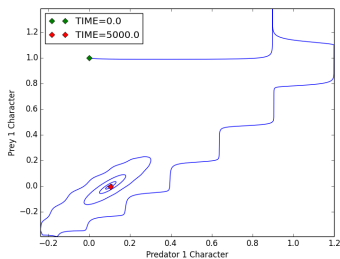
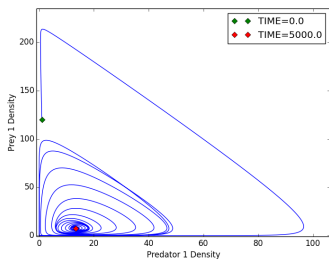
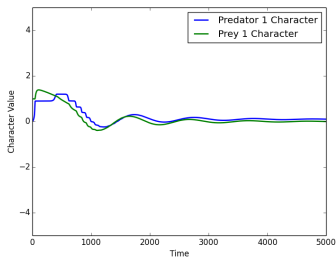
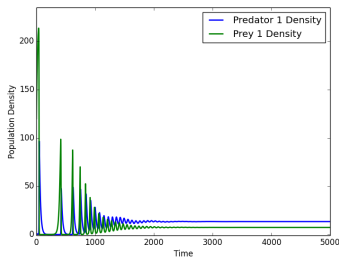
$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \bar{n}} = \beta_G^2 \left[\frac{d\bar{r}}{d\bar{n}} \left(1 - \frac{N}{K} \right) - M \frac{\partial \bar{a}}{\partial \bar{n}} \right]$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \bar{m}} = \sigma_G^2 \left[eN \frac{\partial \bar{a}}{\partial \bar{m}} \right]$$

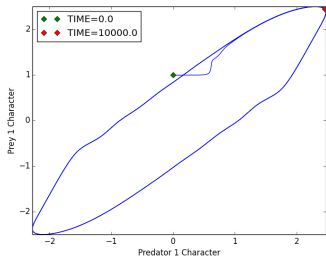
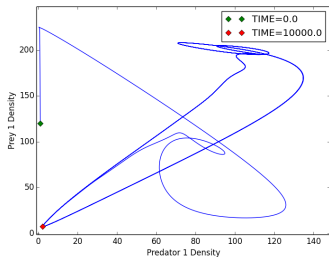
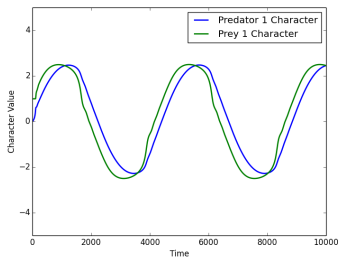
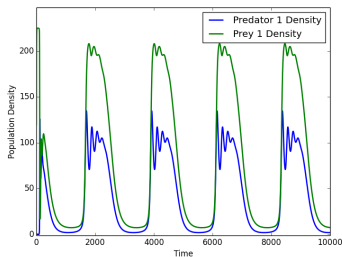
1 × 1 - Stable Exclusion



1 × 1 - Stable Coexistence



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



Future Work

- (1×2) Two predator species in competition for one prey
- (2×1) Two prey species in apparent competition via one generalist predator
- (2×2) One specialist predator competing with one generalist predator for two prey
- (2×3) Two specialist predators competing with one generalist predator for two prey species
- $(u \times v)$ The General Ditrophic Expansion
- Intraguild Predation and General Multitrophic Expansion

Thank You!

- CSUN Chapter of Sigma Xi
- Dr. Daniel Katz, and all other organizers of this Sigma Xi Symposium
- National Science Foundation
- Dr. Helena Noronha
- Pacific Math Alliance PUMP Undergraduate Research Groups
- California State University, Northridge
- Dr. Jing Li and Dr. Casey terHorst

Questions?

Attack Rate

Attack Rate is a Gaussian 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
- $\bar{n} \equiv$ **Average** Prey Trait Value
- $m \equiv$ Predator Trait Value
- $\bar{m} \equiv$ **Average** Predator Trait Value

Parameters

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

Attack Rate

Attack Rate is a Gaussian 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

$$\begin{aligned} \bar{a}(\bar{n}, \bar{m}) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} a(n, m) \cdot p(n, \bar{n}) \cdot p(m, \bar{m}) \, dn \, dm \\ &= \frac{\alpha\tau}{\sqrt{\sigma^2 + \beta^2 + \tau^2}} \exp \left[-\frac{((\bar{m} - \bar{n}) - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)} \right] \end{aligned}$$

Variables

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

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

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

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

Intrinsic Growth Rate

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

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

Average 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

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

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

Variables

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

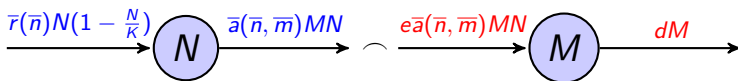
Parameters

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

Ecological Components

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

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Variables

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Evolutionary Components

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

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

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

Variables

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

Parameters

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

Our Proposed 1 × 1 Model - (One Prey Species, One Predator Species)

Ecological Components

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

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

Evolutionary Components

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

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

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \bar{m}}$$

Extinction

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

Exclusion

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

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \bar{m}}$$

Extinction *Unstable*

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

Exclusion

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

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \bar{Y}}{\partial \bar{n}}$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Extinction	<i>Unstable</i>
-------------------	-----------------

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

Exclusion	<i>Locally asymptotically stable under certain conditions</i>
------------------	---

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

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \bar{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction	<i>Unstable</i>
-------------------	-----------------

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

Exclusion	<i>Locally asymptotically stable under certain conditions</i>
------------------	---

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

Necessary Conditions for Local Asymptotically Stable Exclusion:

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

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \bar{m}}$$

Coexistence

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

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

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \bar{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Coexistence	<i>Locally asymptotically stable under certain conditions</i>
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$$(N^*, M^*, \bar{n}^*, \bar{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right), \theta, \theta + \phi \right)$$

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

Equilibria - 1×1

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{n}}{dt} = \beta_G^2 \frac{\partial \bar{Y}}{\partial \bar{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \bar{n}, M, \bar{m})$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Coexistence	<i>Locally asymptotically stable under certain conditions</i>
--------------------	---

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

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

Necessary Condition for Local Asymptotic Stable Coexistence:

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

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

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

↓

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

Predator Fitness

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

Notation

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

Prey Fitness

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

↓

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

Predator Fitness

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

↓

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

Notation

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

Average Fitness

$$\begin{aligned}
 \overline{Y}_j(N_j, \overline{n}_j, [M_i]_{i=1}^u, [\overline{m}_i]_{i=1}^u) \\
 &= \int_{\mathbb{R}^{u+1}} Y_j \cdot \prod_{i=1}^u \left[p_i(m_i, \overline{m}_i) \right] \cdot p(n, \overline{n}) \prod_{i=1}^u [dm_i] dn_j \\
 &= \overline{r}_j(\overline{n}_j) \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u M_i \overline{a}_{ij}(\overline{n}_j, \overline{m}_i)
 \end{aligned}$$

$$\begin{aligned}
 \overline{W}_i(N_j, \overline{n}_j, [M_i]_{i=1}^u, [\overline{m}_i]_{i=1}^u) \\
 &= \int_{\mathbb{R}^{u+1}} W_i \cdot p_i(m_i, \overline{m}_i) \cdot \prod_{j=1}^v \left[p(n_j, \overline{n}_j) \right] dm_i \prod_{j=1}^v [dn_j] \\
 &= \sum_{j=1}^v \left[e_{ij} N_j \overline{a}_{ij}(\overline{n}_j, \overline{m}_i) \right] - d_i
 \end{aligned}$$

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

Ecological Components

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

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

Evolutionary Components

$$\begin{aligned} \frac{d\overline{n_j}}{dt} = \beta_{Gj}^2 \frac{\partial \overline{Y_j}}{\partial \overline{n_j}} = \beta_{Gj}^2 \left[\overline{r_j}(\overline{n_j}) \left(1 - \frac{N_j}{K_j} \right) \frac{(\phi_j - \overline{n_j})}{\beta_j^2 + \gamma_j^2} \right. \\ \left. + \sum_{i=1}^u \left[\frac{M_i(\theta_{ij} - (\overline{m_i} - \overline{n_j}))}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) \right] \right] \end{aligned}$$

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

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

