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

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May 1, 2015

Sigma Xi Student Research Symposium

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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
    - Genetic adaptation is insignificant

Observations in Nature

- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod [Saloniemi, 1993]
  - Classical Lotka-Volterra model
    - Genetic adaptation is insignificant
- There is trait variation within species, which causes **variation in fundametal 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

$$\xrightarrow{\color{blue}{r}N} \boxed{N} \xrightarrow{\color{red}{\alpha}MN} \frown \xrightarrow{e\color{red}{\alpha}MN} \boxed{M} \xrightarrow{dM}$$

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

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

- Prey Exponential Growth
- Predator Exponential Decay
- Linear Functional Response

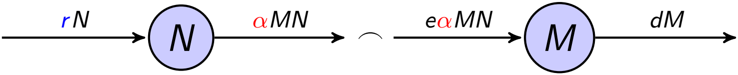
Variables

- $N \equiv$ 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



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

- Prey Exponential Growth
- Predator Exponential Decay
- Linear Functional Response

Variables

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

Parameters

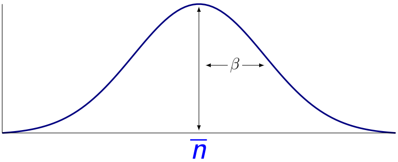
- $\alpha \equiv$ Attack rate $\longleftarrow$ **No variation!**
- $r \equiv$ Prey birth rate $\longleftarrow$ **No variation!**
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

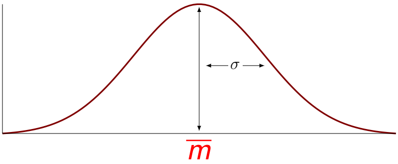
Normally Distributed Trait Values

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

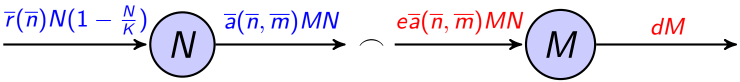
Parameters

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

Ecological Components

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

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



Variables

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

Parameters

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

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

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

Variables

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

Parameters

- $\bar{a}$ ≡ Average Attack Rate **Function**
- $\bar{r}$ ≡ Average Intrinsic Prey Growth Rate **Function**
- β_G^2 ≡ Prey genetic variance
- σ_G^2 ≡ Predator genetic variance

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

Ecological Components

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

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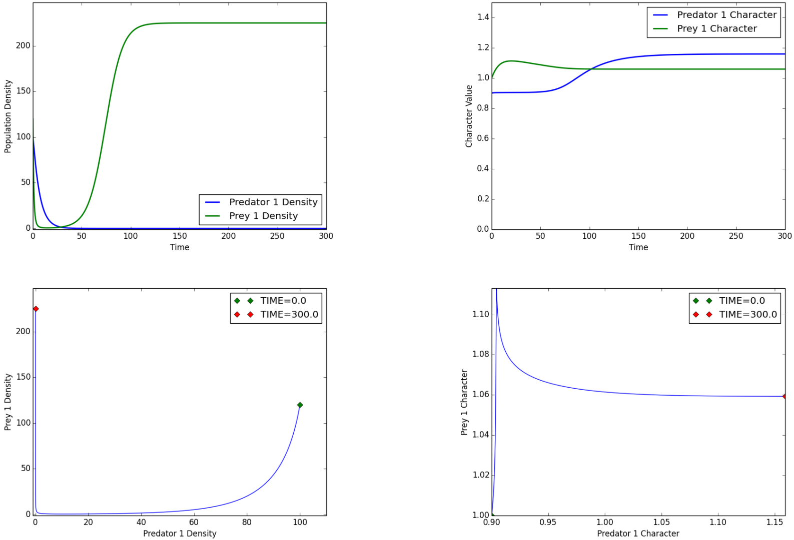
Evolutionary Components

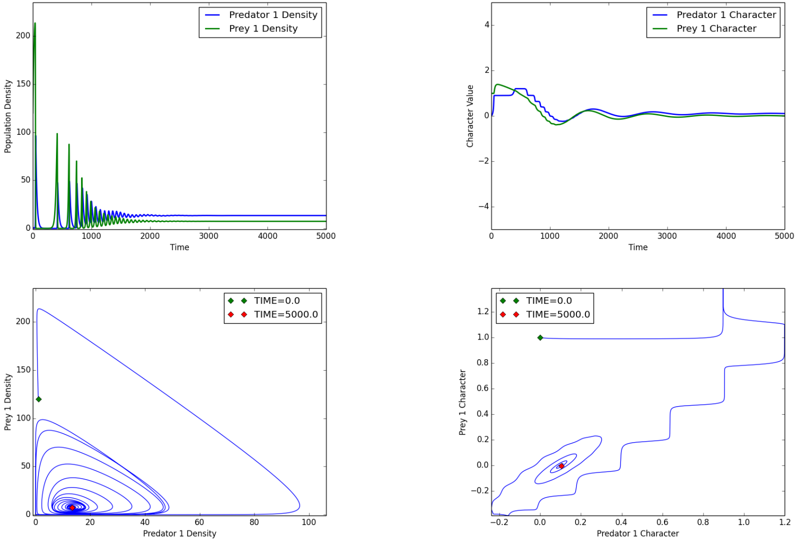
$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \left[\frac{d\overline{r}}{d\overline{n}}\left(1 - \frac{N}{K}\right) - M\frac{\partial \overline{a}}{\partial \overline{n}}\right]$$

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

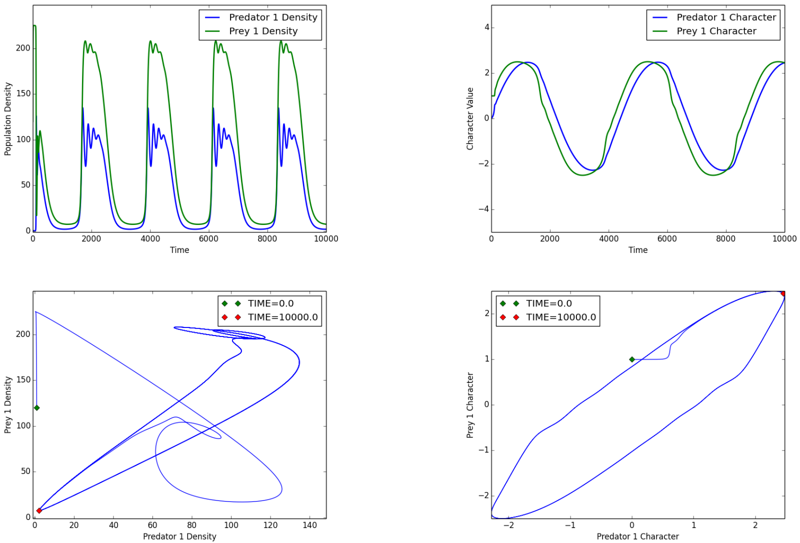
1 × 1 - Stable Exclusion



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
- $\overline{n} \equiv$ **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

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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

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

Variables

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

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

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
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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

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

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

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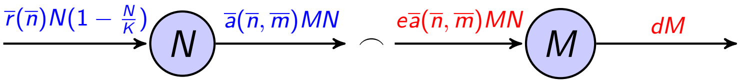

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$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n})$$

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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

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

Ecological Components

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Equilibria - 1 × 1

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

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Extinction

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

Exclusion

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

Equilibria - 1 × 1

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

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

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

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

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Equilibria - 1×1

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

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Extinction *Unstable*

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

Exclusion *Locally asymptotically stable under certain conditions*

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

Necessary Conditions for Local Asymptotically Stable Exclusion:

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

Equilibria - 1×1

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

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Coexistence

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

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

Equilibria - 1 × 1

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

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

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Equilibria - 1 × 1

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

Necessary Condition for Local Asymptotic Stable Coexistence:

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

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

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

$$\downarrow$$

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

Predator Fitness

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

Notation

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

Prey Fitness

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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

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

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

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

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

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

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

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

Ecological Components

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

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

Evolutionary Components

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

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

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