The Effects of Intraspecific Genetic Variation on the Dynamics of Predator-Prey Ecological Communities

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May 3, 2015

Preparing Undergraduates through Mentoring for PhDs (PUMP) Research Symposium

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Supported By:	Pacific Math Alliance, PUMP,	CSU Northridge

Overview

- Motivation
  - Observations in Nature
  - Previous Models
- Our Expansions
  - Gaussian Attack Rate under Coevolution
  - Introduce Stabilizing Selection
  - General Ditrophic Expansion
- Discussion

Observations in Nature

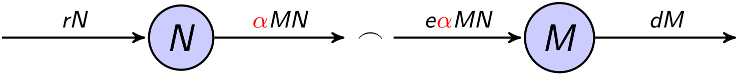
- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod [Saloniemi, 1993]
  - Classical Lotka-Volterra model
    - Genetic adaptation is insignificant

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



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

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

Variables

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

Parameters

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

Classical Lotka-Volterra Model

$$\xrightarrow{rN} \boxed{N} \xrightarrow{\alpha MN} \frown \xrightarrow{e\alpha MN} \boxed{M} \xrightarrow{dM}$$

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

- 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
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

Schreiber, Bürger, and Bolnick's Expansion

Assume the Predator Species has a normally distributed trait value.

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

Parameters

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

Variables

- $m \equiv$ Predator Trait Value

Schreiber, Bürger, and Bolnick's Expansion

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 Expansion

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 Trait Value)))

Parameters

- $\sigma^2 \equiv$ Predator Trait Variance
- $\alpha \equiv$ Maximum attack rate
- $\tau \equiv$ Specialization Constant
- $\theta \equiv$ Optimal trait value
  ↑ **No variation!**

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

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

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

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

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

Fitness Assumptions

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

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

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

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

Average Fitness

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

Variables

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

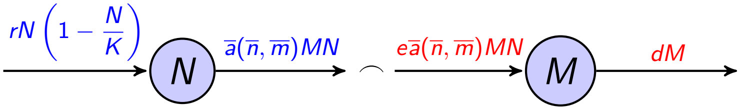
Parameters

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

Ecological Components

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

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



Variables

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

Parameters

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

Evolutionary Components

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

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

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

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 Prey Species, One Predator Species)

Ecological Components

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

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

Evolutionary Components

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

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

Equilibria - 1×1

Extinction

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

Equilibria - 1×1

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

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

Equilibria - 1×1

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

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

Exclusion

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

where μ^* is arbitrary

Equilibria - 1×1

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

Exclusion

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta) \qquad \text{where } \mu^* \text{ is arbitrary}$$

Necessary Condition for Asymptotically $\boxed{\textit{Stable}}$ *Exclusion:*

$$d > \frac{Ke\alpha\tau}{\sqrt{A}} \qquad \text{where A} = \sigma^2 + \beta^2 + \tau^2$$

Equilibria - 1×1

Coexistence

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

Equilibria - 1×1

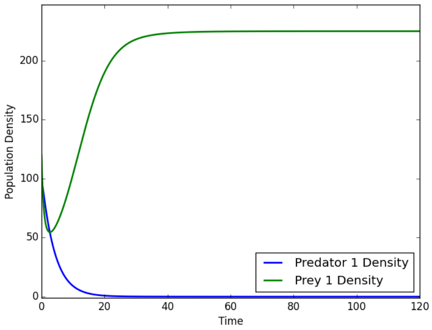
Coexistence

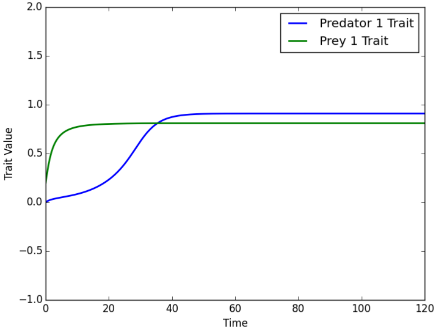
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}\ ,\ \frac{r\sqrt{A}}{\alpha\tau}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)\ ,\ \mu^*\ ,\ \mu^* + \theta\right)$$

Necessary Condition for Asymptotically $\boxed{\textit{Stable}}$ *Coexistence:*

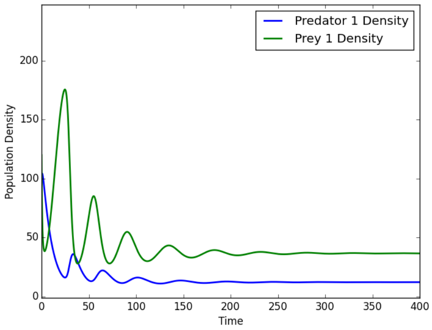
$$\frac{\sigma_G^2}{\beta_G^2} > \frac{r}{d}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)$$

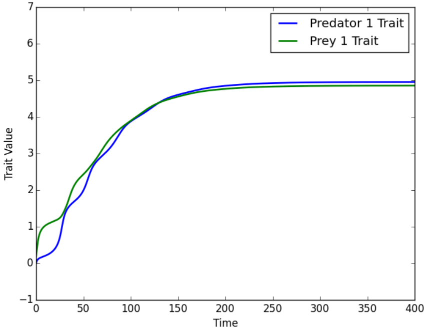
Figures - 1 $\times$ 1 - Stable Exclusion



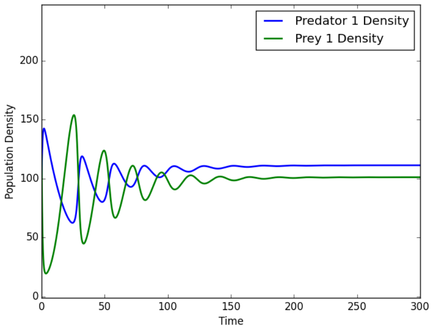


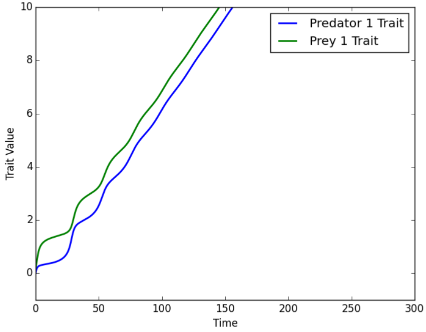
Figures - 1 × 1 - Stable Coexistence





Figures - 1 $\times$ 1 - "Arms Race" Coexistence





Avoiding an "Arms Race" with Stabilizing Selection

Assume Prey Growth Rate is a 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

Avoiding an "Arms Race" with Stabilizing Selection

Assume Prey Growth Rate 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

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

Ecological Components

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

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

Evolutionary Components

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

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

Equilibria - 1×1

Extinction

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

Equilibria - 1×1

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

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

Exclusion

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta) \qquad \text{where } \mu^* \text{ is arbitrary}$$

Equilibria - 1×1

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

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$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta) \qquad \text{where } \mu^* \text{ is arbitrary}$$

Necessary Condition for Asymptotically $\boxed{\textit{Stable}}$ *Exclusion:*

$$d > \frac{Ke\alpha\tau}{\sqrt{A}} \qquad \text{where A} = \sigma^2 + \beta^2 + \tau^2$$

Equilibria - 1×1

Coexistence

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

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

Equilibria - 1×1

Coexistence

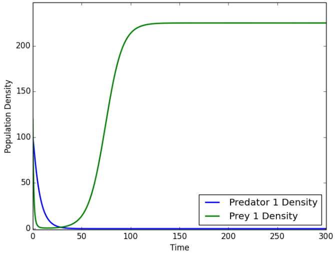
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau} \, , \, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \, , \, \phi \, , \, \theta + \phi \right)$$

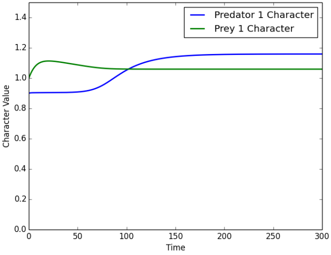
where $A = \sigma^2 + \beta^2 + \tau^2$ and $B = \beta^2 + \gamma^2$

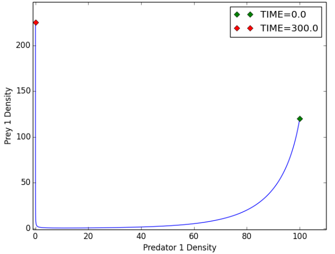
Necessary Condition for Asymptotically $\boxed{\textit{Stable}}$ *Coexistence:*

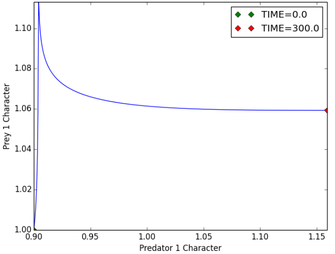
$$\frac{\sigma_G^2}{\beta_G^2} > \frac{\rho\gamma}{d\sqrt{B}} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \left(1 - \frac{A}{B} \right)$$

Figures - 1×1 - Stable Exclusion

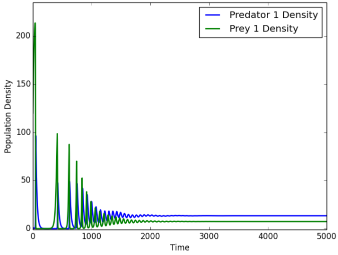


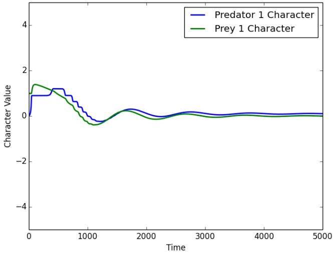


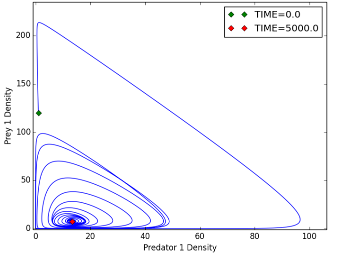


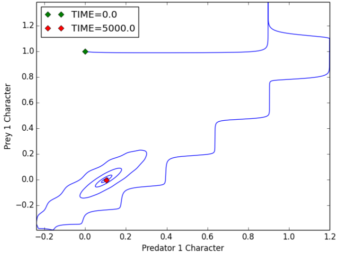


Figures - 1×1 - Stable Coexistence

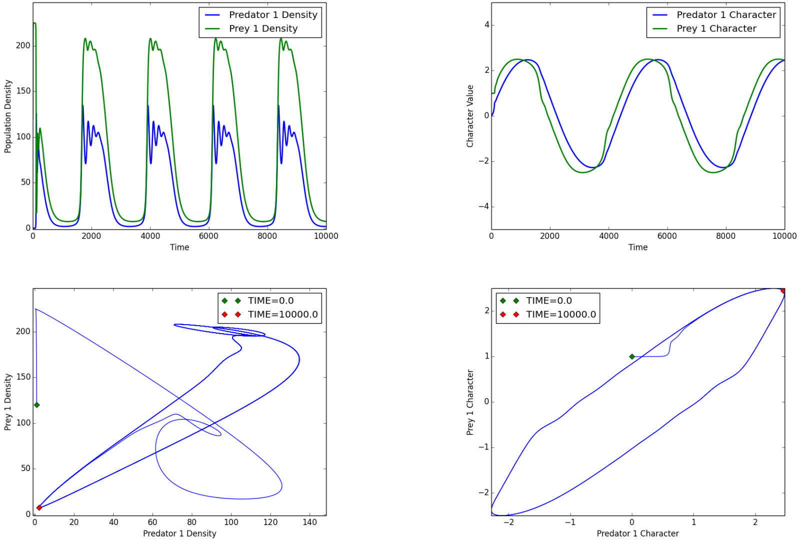




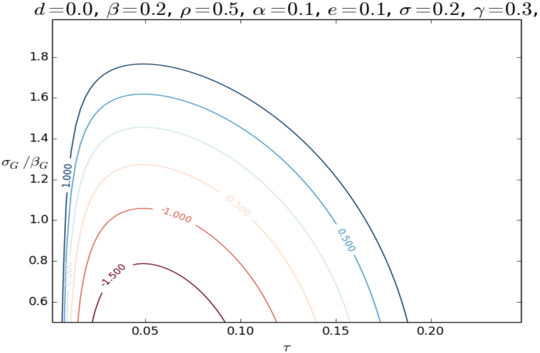




Figures - 1×1 - Stable Cycles (Red Queen Dynamics)[Kindrik, Kondrashov, 1994]



Contour Plot - Coexistence Asymptotic Stability Criterion



$$f_{\text{stable}}(\textit{system parameters}) = \frac{\sigma_G^2}{\beta_G^2} - \frac{\rho\gamma}{d\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)\left(1 - \frac{A}{B}\right)$$

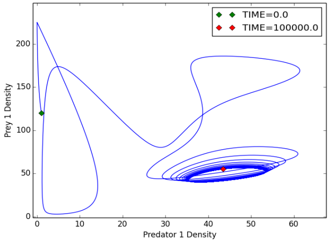
$f_{\text{stable}} > 0 \implies$ Coexistence is *stable*

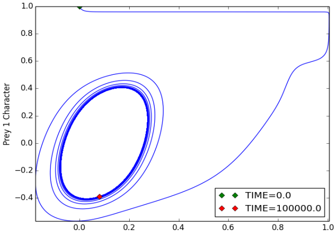
$f_{\text{stable}} < 0 \implies$ Coexistence is *unstable*

$f_{\text{stable}} = 0 \implies$ Hopf Bifurcation

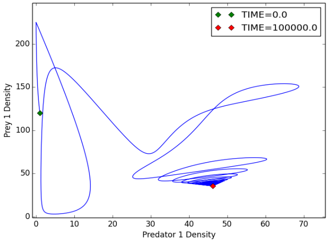
$\tau = 0.05$: Limit Cycle vs. Node

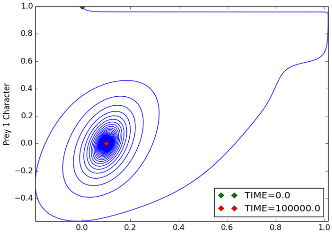
$$\frac{\sigma_G}{\beta_G} = 1.3 \implies f_{\text{stable}} < 0$$





$$\frac{\sigma_G}{\beta_G} = 1.5 \implies f_{\text{stable}} > 0$$





Summary of the 1×1 Model

- 4-dimensional system of ODEs
  - 2 ODEs describing the change in **population size** over time
  - 2 ODEs describing the change in **trait value** over time

Summary of the 1×1 Model

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  - Exclusion (Stable under certain conditions)
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Summary of the 1×1 Model

- 4-dimensional system of ODEs
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- 3 equilibrium points
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  - Exclusion (Stable under certain conditions)
  - Coexistence (Stable under certain conditions)
- Non-Equilibrium Dynamics
  - Constant Growth Rate
    - "Arms Race" Coexistence
  - Gaussian Growth Rate Function
    - Stable Limit Cycles

Expansion of Fitness Functions

Prey Fitness

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

Predator Fitness

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

Expansion of Fitness Functions

Prey Fitness

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$$\downarrow$$

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

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

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

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

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

Average Fitness Calculation

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

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

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

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

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

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

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

Ecological Components

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

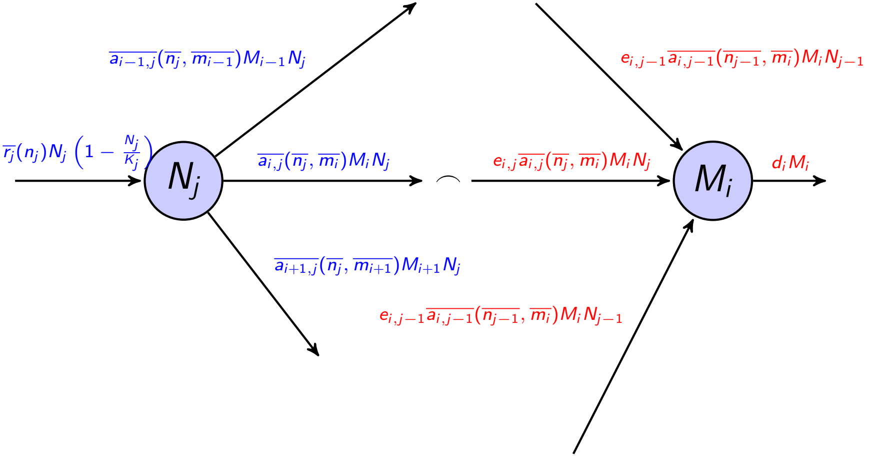
$$\frac{dM_i}{dt} = M_i \overline{W_i} = M_i \left[\sum_{j=1}^{v} \left[e_{ij} N_j \overline{a_{ij}}(\overline{n_j}, \overline{m_i}) \right] - d_i \right]$$

Evolutionary Components

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

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

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



The Complete 2 × 1 Model - (2 Prey Species, 1 Predator Species)

Ecological Components

$$\frac{dN_1}{dt} = N_1\overline{Y_1} = N_1\left[\overline{r_1}(\overline{n_1})\left(1-\frac{N_1}{K_1}\right) - M\overline{a_1}(\overline{n_1},\overline{m})\right]$$

$$\frac{dN_2}{dt} = N_2\overline{Y_2} = N_2\left[\overline{r_2}(\overline{n_2})\left(1-\frac{N_2}{K_2}\right) - M\overline{a_2}(\overline{n_2},\overline{m})\right]$$

$$\frac{dM}{dt} = M\overline{W} = M\left[\sum_{j=1}^{2}\left[e_jN_j\overline{a_j}(\overline{n_j},\overline{m})\right] - d\right]$$

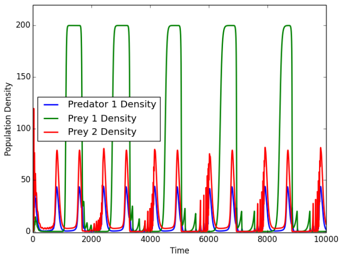
Evolutionary Components

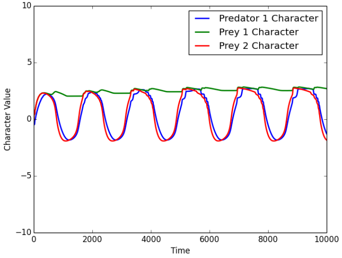
$$\frac{d\overline{n_1}}{dt} = \beta_{G1}^2\frac{\partial\overline{Y_1}}{\partial\overline{n_1}} = \beta_{G1}^2\left[\overline{r_1}(\overline{n_1})\left(1-\frac{N_1}{K_1}\right)\frac{(\phi_1-\overline{n_1})}{\beta_1^2+\gamma_1^2} + \frac{M(\theta_1-(\overline{m}-\overline{n_1}))}{\sigma^2+\beta_1^2+\tau_1^2}\overline{a_1}(\overline{n_1},\overline{m})\right]$$

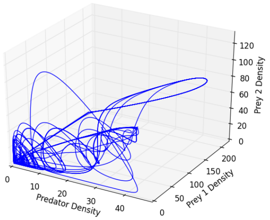
$$\frac{d\overline{n_2}}{dt} = \beta_{G1}^2\frac{\partial\overline{Y_2}}{\partial\overline{n_2}} = \beta_{G2}^2\left[\overline{r_2}(\overline{n_2})\left(1-\frac{N_2}{K_2}\right)\frac{(\phi_2-\overline{n_2})}{\beta_2^2+\gamma_2^2} + \frac{M(\theta_2-(\overline{m}-\overline{n_2}))}{\sigma^2+\beta_2^2+\tau_2^2}\overline{a_2}(\overline{n_2},\overline{m})\right]$$

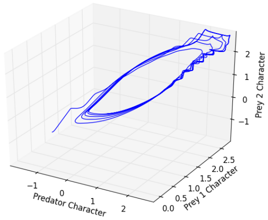
$$\frac{d\overline{m}}{dt} = \sigma_G^2\frac{\partial\overline{W}}{\partial\overline{m}} = \sigma_G^2\sum_{j=1}^{2}\left[\frac{e_jN_j(\theta_j-(\overline{m}-\overline{n_j}))}{\sigma^2+\beta_j^2+\tau_j^2}\overline{a_j}(\overline{n_j},\overline{m})\right]$$

Figures - 2 × 1

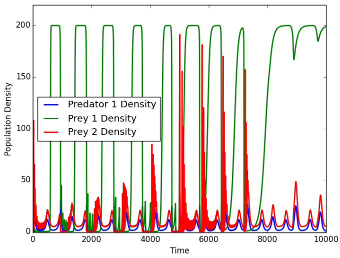

Predator 1 Density
Prey 1 Density
Prey 2 Density
Population Density
Time
0
50
100
150
200
0
2000
4000
6000
8000
10000


Predator 1 Character
Prey 1 Character
Prey 2 Character
Character Value
Time
−10
−5
0
5
10
0
2000
4000
6000
8000
10000


Predator Density
Prey 1 Density
Prey 2 Density
0
10
20
30
40
0
50
100
150
200
0
20
40
60
80
100
120


Predator Character
Prey 1 Character
Prey 2 Character
−1
0
1
2
0.0
0.5
1.0
1.5
2.0
2.5
−1
0
1
2

Figures - 2 × 1


Population Density
Time
Predator 1 Density
Prey 1 Density
Prey 2 Density
0
50
100
150
200
2000
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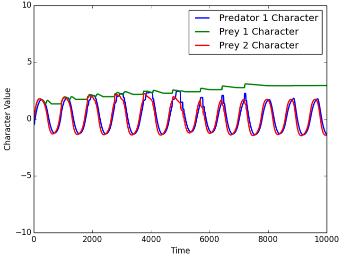
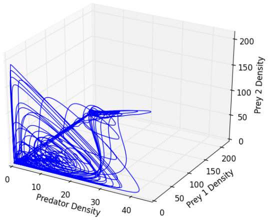
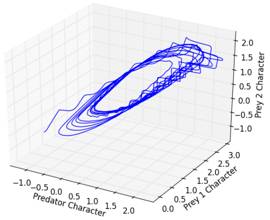
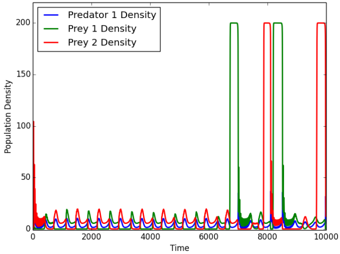
6000
8000
10000

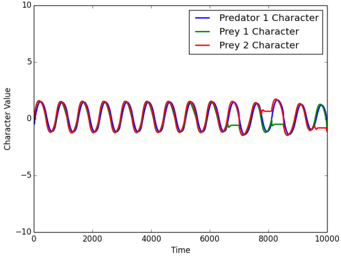

Character Value
Time
Predator 1 Character
Prey 1 Character
Prey 2 Character
10
5
0
−5
−10
2000
4000
6000
8000
10000

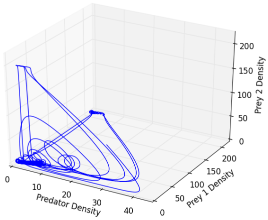

Predator Density
Prey 1 Density
Prey 2 Density

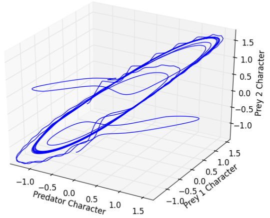

Predator Character
Prey 1 Character
Prey 2 Character

Figures - 2 × 1

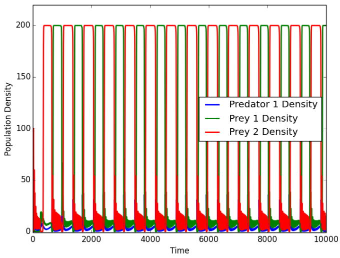

Predator 1 Density
Prey 1 Density
Prey 2 Density
Population Density
Time


Predator 1 Character
Prey 1 Character
Prey 2 Character
Character Value
Time


Predator Density
Prey 1 Density
Prey 2 Density


Predator Character
Prey 1 Character
Prey 2 Character

Figures - 2 × 1


Predator 1 Density
Prey 1 Density
Prey 2 Density
Population Density
Time
0
50
100
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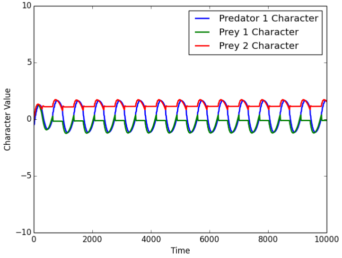
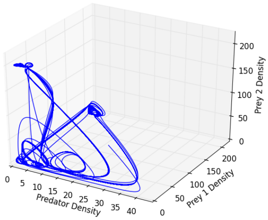
200
0
2000
4000
6000
8000
10000


Predator 1 Character
Prey 1 Character
Prey 2 Character
Character Value
Time
10
5
0
−5
−10
0
2000
4000
6000
8000
10000


Predator Density
Prey 1 Density
Prey 2 Density
0
5
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15
20
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35
40
0
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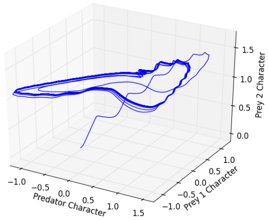
100
150
200
0
50
100
150
200


Predator Character
Prey 1 Character
Prey 2 Character
−1.0
−0.5
0.0
0.5
1.0
1.5
−1.0
−0.5
0.0
0.5
1.0
0.0
0.5
1.0
1.5

The Complete 1 × 2 Model - (1 Prey Species, 2 Predator Species)

Ecological Components

$$\frac{dN}{dt} = N\overline{Y} = N\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right) - \sum_{i=1}^{2} M_i \overline{a_i}(\overline{n}, \overline{m_i})\right]$$

$$\frac{dM_1}{dt} = M_1\overline{W} = M_1\left[e_1 N \overline{a_1}(\overline{n}, \overline{m_1}) - d_1\right]$$

$$\frac{dM_2}{dt} = M_2\overline{W} = M_2\left[e_2 N \overline{a_2}(\overline{n}, \overline{m_2}) - d_2\right]$$

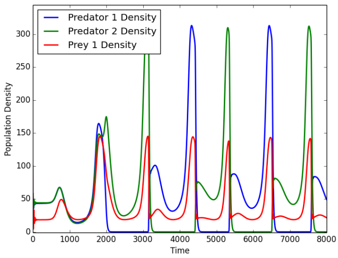
Evolutionary Components

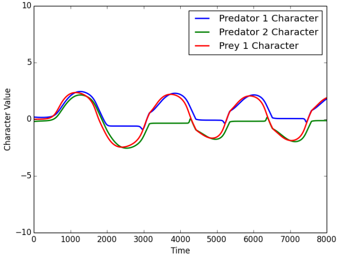
$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2\left[\overline{r}(\overline{n})\left(1 - \frac{N}{K}\right)\frac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \sum_{i=1}^{2}\left[\frac{M_i(\theta_i - (\overline{m_i} - \overline{n}))}{\sigma_i^2 + \beta^2 + \tau_i^2}\overline{a_i}(\overline{n}, \overline{m_i})\right]\right]$$

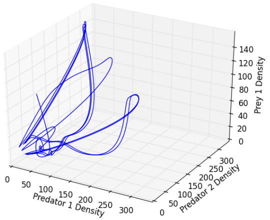
$$\frac{d\overline{m_1}}{dt} = \sigma_{G1}^2 \frac{\partial \overline{W_1}}{\partial \overline{m_1}} = \sigma_{G1}^2\left[\frac{e_1 N(\theta_1 - (\overline{m_1} - \overline{n}))}{\sigma_1^2 + \beta^2 + \tau_1^2}\overline{a_1}(\overline{n}, \overline{m_1})\right]$$

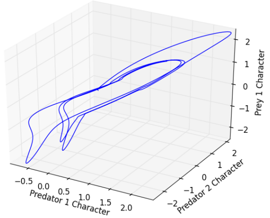
$$\frac{d\overline{m_2}}{dt} = \sigma_{G1}^2 \frac{\partial \overline{W_2}}{\partial \overline{m_2}} = \sigma_{G1}^2\left[\frac{e_2 N(\theta_2 - (\overline{m_2} - \overline{n}))}{\sigma_2^2 + \beta^2 + \tau_2^2}\overline{a_2}(\overline{n}, \overline{m_2})\right]$$

Figures - 1 × 2

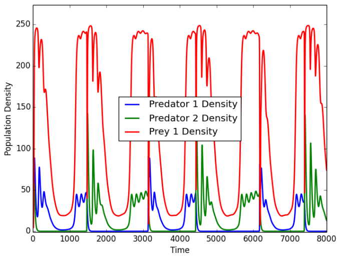

Predator 1 Density
Predator 2 Density
Prey 1 Density
Population Density
Time

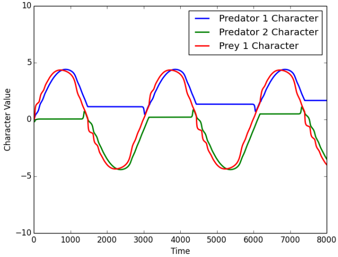

Predator 1 Character
Predator 2 Character
Prey 1 Character
Character Value
Time

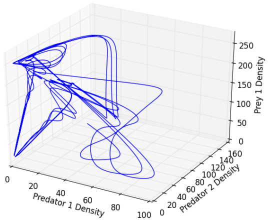

Predator 1 Density
Predator 2 Density
Prey 1 Density

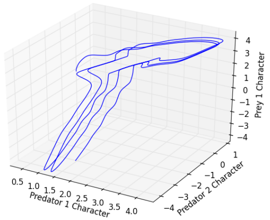

Predator 1 Character
Predator 2 Character
Prey 1 Character

Figures - 1 × 2


Population Density
Time
Predator 1 Density
Predator 2 Density
Prey 1 Density


Character Value
Time
Predator 1 Character
Predator 2 Character
Prey 1 Character


Predator 1 Density
Predator 2 Density
Prey 1 Density


Predator 1 Character
Predator 2 Character
Prey 1 Character

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!

- PUMP (Preparing Undergraduates through Mentoring towards PhDs)
- The Pacific Math Alliance
- The National Math Alliance
- Dr. Helena Noronha, Dr. Ramin Vakilian, and all other PUMP organizers
- National Science Foundation
- California State University, Northridge
- Dr. Jing Li and Dr. Casey terHorst

Questions?