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

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Start Date: March 2014 - - Today's Date: March 26, 2015

The Model

Attack Rate as a Function of Predator and Prey Trait Values

Let $M_i(t)$ be the density of the i^{th} predator species, and let $N_j(t)$ be the density of the j^{th} prey species. Let $\overline{m_i}(t)$ be the mean of a single quantitative trait in the i^{th} predator species, and let $\overline{n_j}(t)$ be the mean of a single quantitative trait in the j^{th} prey species. Suppose the traits are normally distributed, and stay normally distributed, with σ_i^2 as the constant variance of the i^{th} predator species, and with β_j^2 as the constant variance of the j^{th} prey species. Their distributions are given by:

$$p(m_i, \overline{m_i}) = \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp\left[-\frac{(m_i - \overline{m_i})^2}{2\sigma_i^2}\right]$$
$$p(n_j, \overline{n_j}) = \frac{1}{\sqrt{2\pi\beta_j^2}} \exp\left[-\frac{(n_j - \overline{n_j})^2}{2\beta_j^2}\right]$$

Assume all of the species' phenotypic variances have genetic and environment components:

$$\sigma_i^2 = \sigma_{Gi}^2 + \sigma_{Ei}^2$$
$$\beta_j^2 = \beta_{Gj}^2 + \beta_{Ej}^2$$

Let $a_{ij}(m_i, n_j)$ be the attack rate of an individual predator from species i on an individual prey from species j. Supposing the attack rate is optimal at α_{ij} when the predator's trait and prey's trait are at an optimal difference θ_{ij}, and decreases in a Gaussian manner as the trait's deviate from that difference, then

$$a_{ij}(m_i, n_j) = \alpha_{ij} \exp\left[-\frac{((m_i - n_j) - \theta_{ij})^2}{2\tau_{ij}^2}\right]$$

where τ_{ij} determines how phenotypically specialized a predator individual of species i must be to use a prey individual of species j. Let $\overline{a_{ij}}(\overline{m_i}, \overline{n_j})$ be the mean attack rate of predator species i on prey species j. Thus,

$$\begin{aligned}\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} a_{ij}(m_i, n_j) \cdot p(m_i, \overline{m_i}) \cdot p(n_j, \overline{n_j}) dm_i dn_j \\ &= \frac{\alpha_{ij}\tau_{ij}}{\sqrt{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2}} \exp\left[-\frac{((\overline{m_i} - \overline{n_j}) - \theta_{ij})^2}{2(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)}\right]\end{aligned}$$

Fitness Assumptions

Let u be the number of predator species, and let v be the number of prey species. Assuming predators have a linear functional response, convert the consumed prey into offspring with efficiencies e_{ij}, and experience a per-capita mortality rate d_i, then the fitness of a predator with phenotype m_i is

$$W_i(m_i, [N]_1^v, [n]_1^v) = \sum_{j=1}^{v} (e_{ij} a_{ij}(m_i, n_j) N_j) - d_i$$

and thus the mean fitness of the i^{th} predator population is

$$\begin{aligned}
\overline{W_i}(\overline{m_i}, [N]_1^v, [\overline{n}]_1^v) &= \int\limits_{\mathbb{R}^{v+1}} W_i(m_i, [N]_1^v, [n]_1^v) p(m_i, \overline{m_i}) \prod_{j=1}^{v} [p(n_j, \overline{n_j})]\, dm_i \prod_{j=1}^{v} [dn_j] \\
&= \sum_{j=1}^{v} (e_{ij} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) N_j) - d_i
\end{aligned}$$

Suppose prey species j experiences logistic-type growth in the absence of predators with carrying capacity K_j and intrinsic growth rate r_j. However, assume the intrinsic growth rate varies as a function of the prey individual's trait value. Assume the contribution of a prey individual to its population decreases in a Gaussian manner as the trait value deviates away from an optimal trait value for that species, ϕ_j. Let ρ_j be the maximal contribution rate and γ_j be the "cost variance". In other words,

$$r_j(n_j) = \rho_j \exp\left[-\frac{(n_j - \phi_j)^2}{2\gamma_j^2}\right]$$

Thus, the average intrinsic growth rate for the prey population is

$$\begin{aligned}
\overline{r}_j(\overline{n}_j) &= \int_{-\infty}^{\infty} r_j(n_j) p(n_j, \overline{n}_j) dn_j \\
&= \frac{\rho_j \gamma_j}{\sqrt{\beta_j^2 + \gamma_j^2}} \exp\left[-\frac{(n_j - \phi_j)^2}{2(\beta_j^2 + \gamma_j^2)}\right]
\end{aligned}$$

Define the fitness of prey individuals with phenotype n_j as

$$\begin{aligned}
Y_j(N_j, n_j, [M]_1^u, [m]_1^u) &= r_j(n_j)\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} (a_{ij}(m_i, n_j) M_i) \\
&= \rho_j \exp\left[-\frac{(n_j - \phi_j)^2}{2\gamma_j^2}\right]\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} (a_{ij}(m_i, n_j) M_i)
\end{aligned}$$

and thus the mean fitness of the j^{th} prey population is

$$\begin{aligned}
\overline{Y_j}(N_j, \overline{n_j}, [M]_1^u, [\overline{m}]_1^u) &= \int\limits_{\mathbb{R}^{u+1}} Y_j(N_j, n_j, [M]_1^u, [m]_1^u) \prod_{i=1}^{u} [p(m_i, \overline{m_i})]\, p(n_j, \overline{n_j}) \prod_{i=1}^{u} [dm_i]\, dn_j \\
&= \overline{r}_j(\overline{n}_j)\left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) M_i
\end{aligned}$$

Ecological Dynamics

The ecological dynamics of the model (population densities) are given by

$$\begin{cases} \dfrac{dM_i}{dt} &= M_i\overline{W_i}(\overline{m_i}, [N]_1^v, [\overline{n}]_1^v) \\ \dfrac{dN_j}{dt} &= N_j\overline{Y_j}(N_j, \overline{n_j}, [M]_1^u, [\overline{m}]_1^u) \end{cases} \tag{1}$$

Evolutionary Dynamics

Assume the evolution of the mean trait value is always in the direction which increases the mean fitness in the population. Thus the evolutionary dynamics are given by

$$\begin{cases} \dfrac{d\overline{m_i}}{dt} &= \sigma_{Gi}^2 \dfrac{\partial \overline{W_i}}{\partial \overline{m_i}} \\ \dfrac{d\overline{n_j}}{dt} &= \beta_{Gj}^2 \dfrac{\partial \overline{Y_j}}{\partial \overline{n_j}} \end{cases} \tag{2}$$

where

$$\begin{aligned} \frac{\partial \overline{W_i}}{\partial \overline{m_i}} &= \sum_{j=1}^{v} \left[\frac{e_{ij}N_j(\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \cdot \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right] \\ \frac{\partial \overline{Y_j}}{\partial \overline{n_j}} &= \overline{r}_j(\overline{n}_j)\left(1 - \frac{N_j}{K_j}\right) \frac{(\phi_j - \overline{n}_j)}{\beta_j^2 + \gamma_j^2} + \sum_{i=1}^{u} \left[\frac{M_i(\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \cdot \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right] \end{aligned}$$

The 1×1 Model

For example, the 1×1 model is a four-dimensional system given by

$$\begin{cases} f_1 = \dfrac{dM}{dt} &= M\overline{W}(\overline{m}, N, \overline{n}) &= M\left[e\overline{a}(\overline{m}, \overline{n})N - d\right] \\ f_2 = \dfrac{dN}{dt} &= N\overline{Y}(N, \overline{n}, M, \overline{m}) &= N\left[\overline{r}(\overline{n})\left(1 - \dfrac{N}{K}\right) - \overline{a}(\overline{m}, \overline{n})M\right] \\ f_3 = \dfrac{d\overline{m}}{dt} &= \sigma_G^2 \dfrac{\partial \overline{W}}{\partial \overline{m}} &= \sigma_G^2\left[\dfrac{eN(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \cdot \overline{a}(\overline{m}, \overline{n})\right] \\ f_4 = \dfrac{d\overline{n}}{dt} &= \beta_G^2 \dfrac{\partial \overline{Y}}{\partial \overline{n}} &= \beta_G^2\left[\overline{r}(\overline{n})\left(1 - \dfrac{N}{K}\right)\dfrac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \dfrac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \cdot \overline{a}(\overline{m}, \overline{n})\right] \end{cases}$$

Equilibrium Analysis

To find the equilibria of this system, we set each equation to zero, i.e. $f_1 = f_2 = f_3 = f_4 = 0$.

$$f_3 = 0 \implies N = 0 \quad \text{or} \quad \overline{m} - \overline{n} = \theta$$

Let's consider the non-trivial solution, and thus $\overline{m} - \overline{n} = \theta$. Then $\overline{a}(\overline{m}, \overline{n}) = \dfrac{\alpha\tau}{\sqrt{A}}$ where $A = \sigma^2 + \beta^2 + \tau^2$.

$$f_1 = 0 \implies M = 0 \quad \text{or} \quad N = \frac{d}{e\overline{a}(\overline{m}, \overline{n})} = \frac{d\sqrt{A}}{e\alpha\tau}$$

Again, let's consider the non-trivial solution, and thus $\dfrac{d\sqrt{A}}{e\alpha\tau}$.

$$f_4 = 0 \implies N = K \quad \text{or} \quad \overline{n} = \phi$$

Since $M \neq 0$, then $f_2 = 0 \implies N \neq K$. Thus $\overline{n} = \phi$, and thus $\overline{m} = \theta + \phi$ and $\overline{r}(\overline{n}) = \dfrac{\rho\gamma}{\sqrt{B}}$ where $B = \beta^2 + \gamma^2$.

$$f_2 = 0 \implies M = \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{e\alpha\tau K}\right)$$

So the coexistence equilibrium solution is

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

To check for local stability, we find eigenvalues of the Jacobian of the system evaluated at C^*.

$$\begin{cases} \dfrac{\partial f_1}{\partial M} &= e\overline{a}(\overline{m},\overline{n})N - d \\ \dfrac{\partial f_1}{\partial N} &= e\overline{a}(\overline{m},\overline{n})M \\ \dfrac{\partial f_1}{\partial \overline{m}} &= \dfrac{MNe(\theta - (\overline{m}-\overline{n}))}{A}\overline{a}(\overline{m},\overline{n}) \\ \dfrac{\partial f_1}{\partial \overline{n}} &= \dfrac{MNe((\overline{m}-\overline{n}) - \theta)}{A}\overline{a}(\overline{m},\overline{n}) \end{cases}$$

$$\begin{cases} \dfrac{\partial f_2}{\partial M} &= -\overline{a}(\overline{m},\overline{n})N \\ \dfrac{\partial f_2}{\partial N} &= \overline{r}(\overline{n})\left(1 - \dfrac{2N}{K}\right) - \overline{a}(\overline{m},\overline{n})M \\ \dfrac{\partial f_2}{\partial \overline{m}} &= -\dfrac{MN(\theta - (\overline{m}-\overline{n}))}{A}\overline{a}(\overline{m},\overline{n}) \\ \dfrac{\partial f_2}{\partial \overline{n}} &= N\left[\dfrac{\phi - \overline{n}}{B}\overline{r}(\overline{n})\left(1 - \dfrac{N}{K}\right) - \dfrac{M((\overline{m}-\overline{n}) - \theta)}{A}\overline{a}(\overline{m},\overline{n})\right] \end{cases}$$

$$\begin{cases} \dfrac{\partial f_3}{\partial M} &= 0 \\ \dfrac{\partial f_3}{\partial N} &= \dfrac{\sigma_G^2 e\overline{a}(\overline{m},\overline{n})(\theta - (\overline{m}-\overline{n})}{A} \\ \dfrac{\partial f_3}{\partial \overline{m}} &= -\dfrac{\sigma_G^2 e\overline{a}(\overline{m},\overline{n})N}{A}\left[1 - \dfrac{(\overline{m}-\overline{n}-\theta)^2}{A}\right] \\ \dfrac{\partial f_3}{\partial \overline{n}} &= \dfrac{\sigma_G^2 e\overline{a}(\overline{m},\overline{n})N}{A}\left[1 - \dfrac{(\overline{m}-\overline{n}-\theta)^2}{A}\right] \end{cases}$$

$$\begin{cases} \dfrac{\partial f_4}{\partial M} &= \dfrac{\beta_G^2 \overline{a}(\overline{m},\overline{n})(\theta - (\overline{m}-\overline{n}))}{A} \\ \dfrac{\partial f_4}{\partial N} &= -\dfrac{\beta_G^2 \overline{r}(\overline{n})(\phi - \overline{n})}{kB} \\ \dfrac{\partial f_4}{\partial \overline{m}} &= -\dfrac{\beta_G^2 \overline{a}(\overline{m},\overline{n})M}{A}\left[1 - \dfrac{(\overline{m}-\overline{n}-\theta)^2}{A}\right] \\ \dfrac{\partial f_4}{\partial \overline{n}} &= \dfrac{\beta_G^2 \overline{r}(\overline{n})\left(1 - \dfrac{N}{K}\right)}{B}\left[\dfrac{(\phi - \overline{n})^2}{B} - 1\right] + \dfrac{\beta_G^2 \overline{a}(\overline{m},\overline{n})M}{A}\left[1 - \dfrac{(\overline{m}-\overline{n}-\theta)^2}{A}\right] \end{cases}$$

Special Case: $M^* = \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), N = \frac{d\sqrt{A}}{Ke\alpha\tau}$

$E^* = (\frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \frac{d\sqrt{A}}{Ke\alpha\tau}, \theta + \phi, \phi)$. Then $J^* = J\big|_{E^*} =$

$$\begin{pmatrix} 0 & \frac{e\rho\gamma}{\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right) & 0 & 0 \\ -\frac{d}{e} & -\frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}} & 0 & 0 \\ 0 & 0 & -\frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ 0 & 0 & -\frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{A\sqrt{B}} & \frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{\sqrt{B}}\left[\frac{1}{A} - \frac{1}{B}\right] \end{pmatrix}$$

The characteristic polynomial is

$$P(\lambda) = |\lambda I - J^*| = \begin{vmatrix} \lambda & \frac{e\rho\gamma}{\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right) & 0 & 0 \\ -\frac{d}{e} & \lambda + \frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}} & 0 & 0 \\ 0 & 0 & \lambda + \frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ 0 & 0 & -\frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{A\sqrt{B}} & \lambda - \frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{\sqrt{B}}\left[\frac{1}{A} - \frac{1}{B}\right] \end{vmatrix}$$

Thus,

$$P(\lambda) = \begin{vmatrix} \lambda & \frac{e\rho\gamma}{\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right) \\ -\frac{d}{e} & \lambda + \frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}} \end{vmatrix} \cdot \begin{vmatrix} \lambda + \frac{\sigma_G^2 d}{A} & \frac{\sigma_G^2 d}{A} \\ -\frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{A\sqrt{B}} & \lambda - \frac{\beta_G^2\rho\gamma\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)}{\sqrt{B}}\left[\frac{1}{A} - \frac{1}{B}\right] \end{vmatrix}$$

$= P_1(\lambda) \cdot P_2(\lambda)$

Thus the zeros of $P(\lambda)$ are the zeros of both $P_1(\lambda)$ and $P_2(\lambda)$.

$$P_1(\lambda) = \lambda^2 + \lambda\frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}} + \frac{d\rho\gamma}{\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right)$$

$$\implies \lambda_{1,2} = \frac{1}{2}\left[-\frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}} \pm \sqrt{\Delta}\right]$$

Where $\Delta = \left(\dfrac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}}\right)^2 - \dfrac{4d\rho\gamma}{\sqrt{B}}\left(1-\dfrac{d\sqrt{A}}{Ke\alpha\tau}\right)$. Since $N^* = \dfrac{d\sqrt{A}}{e\alpha\tau} < K$, $\sqrt{\Delta} < \left|\dfrac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}}\right|$. Thus $\mathrm{Re}(\lambda_{1,2}) < 0 \iff \left(\dfrac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}}\right)^2 > \dfrac{4d\rho\gamma}{\sqrt{B}}\left(1-\dfrac{d\sqrt{A}}{Ke\alpha\tau}\right)$. So the coexistence equilibrium is stable if

$$\left(\frac{d\rho\gamma\sqrt{A}}{Ke\alpha\tau\sqrt{B}}\right)^2 > \frac{4d\rho\gamma}{\sqrt{B}}\left(1-\frac{d\sqrt{A}}{Ke\alpha\tau}\right)$$

For simplicity, let $C = \dfrac{d\sigma_G^2}{A}$, $\quad D = \dfrac{\beta_G^2\rho\gamma\left(1-\dfrac{d\sqrt{A}}{Ke\alpha\tau}\right)}{A\sqrt{B}}$, $\quad E = \dfrac{\beta_G^2\rho\gamma\left(1-\dfrac{d\sqrt{A}}{Ke\alpha\tau}\right)}{B^{3/2}}$

$$\begin{aligned} P_2(\lambda) &= \lambda^2 + (C+E-D)\lambda + CE = 0 \\ \implies \lambda_{3,4} &= \frac{1}{2}\left[-(C+E-D) \pm \sqrt{\Delta}\right] \end{aligned}$$

Where

$$\Delta = (C+E-D)^2 - 4CE$$

Again, since $N^* = \dfrac{d\sqrt{A}}{e\alpha\tau} < K$ and $C, D, E > 0$, $\sqrt{\Delta} < |C+E-D|$. Thus $\mathrm{Re}(\lambda_{3,4}) < 0 \iff C+E > D$ and $C^2+D^2+E^2 > 2(CD+DE+CE)$. So the coexistence equilibrium is stable if

$$\begin{aligned} C+E &> D \\ C^2+D^2+E^2 &> 2(CD+DE+CE) \end{aligned}$$