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

Sam Fleischer, Pablo Chavarria, Casey terHorst, Jing Li
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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

$$\frac{\partial \overline{W_i}}{\partial \overline{m_i}} = \sum_{j=1}^{v} \left[\frac{e_{ij}N_j(\theta_{ij} - (\overline{m}_i - \overline{n}_j))}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \cdot \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) \right]$$

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

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 $A = \alpha^2 + \beta^2 + \tau^2$.

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

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 $\overline{r}(\overline{n}) = \rho$.

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

So the coexistence equilibrium solution is

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

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

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

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