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

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The Model

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, 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.

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

All of the species' phenotypic variances have a genetic and environment component,

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

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 diverge 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,

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

Let u be the number of predator species, and let v be the number of prey species. If 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

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

In the absence of the predators, each prey experience logistic growth with varying intrinsic growth rates $r_j(n_j)$ and carrying capacities K_j. Assume the intrinsic growth rate of each prey decreases in a Gaussian manner as the the prey trait value diverges away from an optimal trait value for that species, ϕ_j. Let ρ_j be the maximal intrinsic growth rate and γ_j be the "cost variance". In other words,

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

The average intrinsic growth rate for the prey population is given by

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

Thus the fitness of a prey with phenotype n_j is

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

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

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

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

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

We assume the distribution of phenotypes remains Gaussian. 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 is a four-dimensional system given by

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