

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

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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  $i^{\text{th}}$  predator species, and let  $N_j(t)$  be the density of the  $j^{\text{th}}$  prey species. Let  $\bar{m}_i(t)$  be the mean of a single quantitative trait in the  $i^{\text{th}}$  predator species, and let  $\bar{n}_j(t)$  be the mean of a single quantitative trait in the  $j^{\text{th}}$  prey species. Suppose the traits are normally distributed, and stay normally distributed, with  $\sigma_i^2$  as the constant variance of the  $i^{\text{th}}$  predator species, and with  $\beta_j^2$  as the constant variance of the  $j^{\text{th}}$  prey species. Their distributions are given by:

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

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  $\alpha_{ij}$  when the predator's trait and prey's trait are at an optimal difference  $\theta_{ij}$ , 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  $\tau_{ij}$  determines how phenotypically specialized a predator individual of species  $i$  must be to use a prey individual of species  $j$ . Let  $\bar{a}_{ij}(\bar{m}_i, \bar{n}_j)$  be the mean attack rate of predator species  $i$  on prey species  $j$ . Thus,

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

## 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  $i^{\text{th}}$  predator population is

$$\begin{aligned} \overline{W}_i(\overline{m}_i, [N]_1^v, [\overline{n}]_1^v) &= \int_{\mathbb{R}^{v+1}} W_i(m_i, [N]_1^v, [n]_1^v) p(m_i, \overline{m}_i) \prod_{j=1}^v [p(n_j, \overline{n}_j)] dm_i \prod_{j=1}^v [dn_j] \\ &= \sum_{j=1}^v (e_{ij} \overline{a}_{ij}(\overline{m}_i, \overline{n}_j) N_j) - d_i \end{aligned}$$

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,  $\phi_j$ . Let  $\rho_j$  be the maximal contribution rate and  $\gamma_j$  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

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

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  $j^{\text{th}}$  prey population is

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

## Ecological Dynamics

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

$$\begin{cases} \frac{dM_i}{dt} &= M_i \bar{W}_i(\bar{m}_i, [N]_1^v, [\bar{n}]_1^v) \\ \frac{dN_j}{dt} &= N_j \bar{Y}_j(N_j, \bar{n}_j, [M]_1^u, [\bar{m}]_1^u) \end{cases} \quad (1)$$

## 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

$$\begin{cases} \frac{d\bar{m}_i}{dt} &= \sigma_{G_i}^2 \frac{\partial \bar{W}_i}{\partial \bar{m}_i} \\ \frac{d\bar{n}_j}{dt} &= \beta_{G_j}^2 \frac{\partial \bar{Y}_j}{\partial \bar{n}_j} \end{cases} \quad (2)$$

where

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

## The $1 \times 1$ Model

For example, the  $1 \times 1$  model is a four-dimensional system given by

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