

Appendix B from S. J. Schreiber and E. Saltzman, “Evolution of Predator and Prey Movement into Sink Habitats”

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Invasion Exponents and Selection for Slower Dispersers

Invasion Exponents

To define the prey and predator invasion exponents, consider a prey-predator population, with abundances (N_1 , N_2 , P_1 , P_2), that has been playing the dispersal strategy (m , μ) sufficiently long for the ecological dynamics to settle on its asymptotic state (e.g., an equilibrium or a periodic orbit). In the initial phase of their invasion, the dynamics of the mutant population are well approximated by the linear system of differential equations

$$\begin{bmatrix} \frac{d\tilde{N}_1}{dt} \\ \frac{d\tilde{N}_2}{dt} \end{bmatrix} = \mathbf{A}_{\text{prey}}(t) \begin{bmatrix} \tilde{N}_1 \\ \tilde{N}_2 \end{bmatrix},$$

where

$$\mathbf{A}_{\text{prey}}(t) = \begin{bmatrix} b_1 \left(1 - \frac{N_1(t)}{K_1} \right) - d_1 - \frac{aP_1(t)}{1 + hN_1(t)} - \tilde{m} & \tilde{m} \\ \tilde{m} & r_2 - \frac{aP_2(t)}{1 + hN_2(t)} - \tilde{m} \end{bmatrix}$$

and $(N_1(t), N_2(t), P_1(t), P_2(t))$ corresponds to the resident system. Let $\Phi_{\text{prey}}(t)$ be a time-varying matrix such that $\Phi_{\text{prey}}(0)$ is the identity matrix and $(d/dt)\Phi_{\text{prey}} = \mathbf{A}_{\text{prey}}(t)\Phi_{\text{prey}}$. Whenever the limit exists, we define the invasion exponent of the mutant prey as

$$\mathcal{I}_{\text{prey}}(m, \tilde{m}) = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \|\Phi_{\text{prey}}(t)\|,$$

where $\|\mathbf{A}(t)\|$ denotes the operator norm of the fundamental matrix $\Phi_{\text{prey}}(t)$. If the invasion exponent $\mathcal{I}_{\text{prey}}$ is positive (respectively, negative), then the mutant prey can (respectively, cannot) invade the resident population. If the resident population is at an equilibrium, then $\mathbf{A}(t)$ does not vary in time, and the invasion exponent is given by the stability modulus $\rho(\mathbf{A})$ of \mathbf{A} : the largest real part of the eigenvalues of \mathbf{A} (see, e.g., Smith 1995).

We can define the predator invasion exponent in a similar manner. Namely, if a rare mutant population of predators the dispersal strategy $\tilde{\mu}$ appears in the resident population, then we define the predator invasion exponent as

$$\mathcal{I}_{\text{pred}}(\mu, \tilde{\mu}) = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \|\Phi_{\text{pred}}(t)\|,$$

where $\Phi_{\text{pred}}(0)$ is the identity matrix, $(d/dt)\Phi_{\text{pred}} = \mathbf{A}_{\text{pred}}(t)\Phi_{\text{pred}}$, and

$$\mathbf{A}_{\text{pred}}(t) = \begin{bmatrix} \frac{\theta a N_1(t)}{1 + h a N_1(t)} - \delta_1 - \tilde{\mu} & \tilde{\mu} \\ \tilde{\mu} & \frac{\theta a N_2(t)}{1 + h a N_2(t)} - \delta_2 - \tilde{\mu} \end{bmatrix}.$$

Selection against Dispersal

Here, we provide a general argument for the evolution of slower dispersers in temporally homogenous environments with n patches. Consider a one-parameter family of matrices

$$\mathbf{B}(\tilde{m}) = \mathbf{D} + \tilde{m}\mathbf{M},$$

where \mathbf{D} is a nonscalar $n \times n$ diagonal matrix and \mathbf{M} is an irreducible matrix with zero column sums and nonnegative off-diagonal elements. One should think of the diagonal entries of \mathbf{D} corresponding to the per capita growth rates in the different patches. The off-diagonal entries of \mathbf{M} correspond to normalized per capita immigration rates, and the diagonal entries of \mathbf{M} correspond to normalized per capita emigration rates.

For example, the invasion exponent for the prey is determined by the matrix

$$\mathbf{A} = \begin{bmatrix} b_1 \left(1 - \frac{N_1}{K_1}\right) - d_1 - \frac{aP_1}{1 + h a N_1} - \tilde{m} & \tilde{m} \\ \tilde{m} & r_2 - \frac{aP_2}{1 + h a N_2} - \tilde{m} \end{bmatrix},$$

and this matrix can be rewritten as

$$\mathbf{A} = \underbrace{\begin{bmatrix} b_1 \left(1 - \frac{N_1}{K_1}\right) - d_1 - \frac{aP_1}{1 + h a N_1} & 0 \\ 0 & r_2 - \frac{aP_2}{1 + h a N_2} \end{bmatrix}}_{\mathbf{D}} + \tilde{m} \underbrace{\begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}}_{\mathbf{M}}.$$

Under equilibrium conditions for the resident population, the per capita growth rates are positive in patch type 1 and negative in patch type 2. Hence, \mathbf{D} is not a scalar matrix.

We will show that the stability modulus $\rho(\mathbf{B}(\tilde{m}))$ of $\mathbf{B}(\tilde{m})$ is a strictly decreasing function of m . In the case of our models, this fact implies that the invasion exponent $\mathcal{I}_{\text{prey}}(m, \tilde{m})$ is a decreasing function of \tilde{m} whenever the resident population playing strategy m is at equilibrium. Because $\mathcal{I}_{\text{prey}}(m, m) = 0$, it follows that $\mathcal{I}_{\text{prey}}(m, \tilde{m}) < 0$ whenever $\tilde{m} > m$ and $\mathcal{I}_{\text{prey}}(m, \tilde{m}) > 0$ whenever $\tilde{m} < m$. In other words, the faster dispersers cannot invade the equilibrium determined by the slower dispersers, while slower dispersers can invade the equilibrium determined by faster dispersers. This implication is biologically meaningful only when the equilibrium determined by the resident populations is stable. A similar argument applies to the predator invasion rates.

Let $f(\tilde{m}) = \rho(\mathbf{B}(\tilde{m}))$. We will show that $f'(\tilde{m}) < 0$. Given any $\tilde{m} = x > 0$, choose $a > 0$ such that $ax\mathbf{I} \geq \min\{D, 0\} + x \min\{M, 0\}$, where \mathbf{I} is the $n \times n$ identity matrix. Define

$$\mathbf{\Lambda} = \frac{1}{x}\mathbf{D} + a\mathbf{I},$$

$$g(t) = \rho(\mathbf{\Lambda} + t\mathbf{M}).$$

Our choice of a and our assumption that \mathbf{M} is irreducible imply that $\mathbf{M} + \mathbf{\Lambda}$ is a nonnegative irreducible matrix. Moreover, because the column sums of \mathbf{M} are 0, the column sums of $\mathbf{M} + \mathbf{\Lambda}$ equal the diagonal entries of $\mathbf{\Lambda}$. The following Lemma from Kirkland et al. (2006), applied to $\mathbf{\Lambda} + t\mathbf{M} = (1 - t)\mathbf{\Lambda} + t(\mathbf{M} + \mathbf{\Lambda})$, implies that $g'(1) < 0$.

Lemma. Suppose that \mathbf{A} is an irreducible nonnegative matrix, and let $\mathbf{D}_\mathbf{A}$ be the diagonal matrix of column sums of \mathbf{A} . Let $\mathbf{\Lambda}$ be a diagonal matrix such that $\mathbf{\Lambda} \geq \mathbf{D}_\mathbf{A}$. For $0 \leq t \leq 1$, let $h(t) = \lambda[(1 - t)\mathbf{A} + t\mathbf{\Lambda}]$. Then $h'(1) < 0$.

Because

$$\begin{aligned} g(t) &= \frac{\rho(x\mathbf{A} + tx\mathbf{M})}{x} \\ &= \frac{\rho(\mathbf{D} + ax\mathbf{I} + tx\mathbf{M})}{x} \\ &= \frac{\rho(\mathbf{D} + tx\mathbf{M})}{x} + a \\ &= \frac{f(xt)}{x} + a, \end{aligned}$$

it follows that $g'(1) = f'(x) < 0$. Because $x = \tilde{m} > 0$ was arbitrary, $f(\tilde{m})$ is a decreasing function of $\tilde{m} > 0$ as claimed.

Literature Cited Only in Appendix B

Smith, H. L. 1995. Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems. Mathematical Surveys and Monographs. Vol. 41. American Mathematical Society, Providence, RI.