Appendix to *Handling time promotes the coevolution of aggregation in predator-prey systems*

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**APPENDIX A: Including Predator Handling Time**

To describe the within generation behavioral dynamics of the predators, let $\tau$ represent time between generations and $T_i$ denote the number of predators handling prey from patch $i$. If predators in generation $t$ are encountering prey in patch $i$ at a rate of $a_i\alpha_iN_t$ and have a mean handling time of $b_i$ for prey in patch $i$, then the behavioral dynamics of the predators are given by

\[
\frac{dS}{d\tau} = -\sum_{i=1}^{n} a_i\alpha_iN_t\beta_iS + \sum_{i=1}^{n} T_i/b_i \\
\frac{dT_i}{d\tau} = a_i\alpha_iN_t\beta_iS - T_i/b_i
\]

(1)

(2)

Since the behavioral dynamics occur rapidly relative to the generation time, they equilibrate. $\frac{dT_i}{dT} = 0$ implies that $T_i = b_i a_i \alpha_i N_t \beta_i S$. Since $P_t = \sum_i H_i + S = \sum_i b_i a_i \alpha_i N_t \beta_i S + S$, we get $S = \frac{P_t}{1 + \sum_i b_i a_i \alpha_i \beta_i N_t}$.

**APPENDIX B: The CoESS**

**The CoESS.** Due to the nonlinearity of $I_P$ with respect to $\tilde{\beta}$, we use the method of Lagrange multipliers to identify the coESS. According to this method a coESS $(\alpha, \beta)$ must satisfy

$$\frac{\partial I_N}{\partial \alpha} (\alpha, \beta; \alpha) = \rho (1, \ldots, 1)$$

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and
\[
\frac{\partial I_P}{\partial \beta}(\alpha, \beta; \beta) = \rho_2(1, \ldots, 1)
\]
for an appropriate choice Lagrange multiplies \(\rho_1\) and \(\rho_2\). Since the system is at equilibrium, we know that
\[
I_N(\alpha, \beta; \alpha) = 1,
\]
namely that \(\sum_{i=1}^{n} \lambda_i \alpha_i \exp(-a_i \beta_i \hat{S}) = 1\). From the Lagrange condition
\[
\frac{\partial I_N}{\partial \alpha_i} = \lambda_i \exp(-a_i \beta_i \hat{S})
\]
which must equal the Lagrange multiplier \(\rho_2\). Since the system is at equilibrium we have
\[
\frac{\hat{P}}{\hat{N}} = \sum_{i=1}^{n} \theta_i \alpha_i (1 - \exp(-a_i \beta_i \hat{S}))
\]
Using the additional facts that \(\frac{\hat{P}}{1 + \sum_{j=1}^{n} a_j b_j \alpha_j \beta_j \hat{S}} = \hat{S}\) and \(\exp(-a_i \beta_i \hat{S}) = \frac{1}{\lambda_i}\) yields
\[
\rho_2 \frac{\hat{N}}{\hat{P}} = -\frac{\hat{P}}{\hat{N}} a_i b_i \alpha_i + \frac{\theta_i \alpha_i}{\beta_i} \left( 1 - \frac{1}{\lambda_i} \right)
\]
Hence,
\[
\alpha_i = \frac{\rho_2 \frac{\hat{N}}{\hat{P}}}{\frac{\theta_i}{\beta_i} \left( 1 - \frac{1}{\lambda_i} \right) - \hat{S}a_i b_i}
\]
where
\[ \rho_2 \frac{\hat{N}}{\bar{p}} = \sum_{i=1}^{n} \theta_i \left( 1 - \frac{1}{\lambda_i} \right) - \hat{S}_{ai} b_i \]

It can be shown through more manipulation of the \( \alpha_i \) expression that
\[ \alpha_i = \frac{\hat{N}_i}{\sum_{i=1}^{n} \hat{N}_i} \]

where
\[ \hat{N}_i = \frac{\hat{S}_i}{\theta_i \left( 1 - \frac{1}{\lambda_i} \right) - \hat{S}_{ai} b_i} \]

Moreover,
\[ \sum_{i=1}^{n} \hat{N}_i = \hat{N} \]

**Prey aggregation.** We verify the claim that long predator handling times promote the coevolution of prey aggregation. Assume that \( a_1 = a_2 = \ldots = a_n = a \) and \( b_1 = b_2 = \ldots = b_n = b \). Define
\[ k_i = \frac{\ln \lambda_i}{a \theta_i (1 - 1/\lambda_i)} \]

for all \( i \). \( k_i \) equals to \( 1/\hat{N}_i \) when \( b = 0 \). Assume that \( k_1 < k_2 < \ldots < k_n \). Define
\[ g_i(b) = \frac{\hat{N}_i}{\hat{N}_{i+1}} = \frac{k_{i+1} - b}{k_i - b} \]

Since \( k_{i+1} > k_i \), \( g'_i(b) = \frac{k_{i+1} - k_i}{(k_i - b)^2} \) and \( g''_i(b) = \frac{2(k_{i+1} - k_i)}{(k_i - b)^3} \), \( g_i \) is increasing and convex on the interval \( [0, b_i] \) and has a vertical asymptote at \( b = k_i \).

**Contrary choices.** We verify if \( \theta_1 = c \lambda_1, \ldots, \theta_n = c \lambda_n \) for some \( c > 0 \), \( b_1 = \ldots = b_n = b \), \( a_1 = \ldots = a_n = a \), and \( \lambda_1 > \lambda_2 > \ldots > \lambda_n \), then \( \hat{N}_1 < \hat{N}_2 < \ldots < \hat{N}_n \). Define
\[ f(\lambda) = \frac{\ln \lambda}{ac(\lambda - 1) - ab \ln \lambda} \]

Taking the derivative yields
\[ f'(\lambda) = \frac{c(1/\lambda + 1 - \ln \lambda)}{a(c (-1 + \lambda) - b \ln \lambda)^2} \]

Let \( g(\lambda) = -1/\lambda + 1 - \ln \lambda \). Since \( g(1) = 0 \) and \( g'(\lambda) < 0 \) for \( \lambda > 1 \), \( f'(\lambda) < 0 \) for all \( \lambda > 1 \) for which it is defined. Since \( \hat{N}_i = f(\lambda_i) \) and \( \lambda_1 > \ldots > \lambda_n \), it follows that \( \hat{N}_1 < \ldots < \hat{N}_n \).
APPENDIX C: Ecological Stability

Let \( f(N, P) = N \sum_{i=1}^{n} \lambda_i \alpha_i \exp(-a_i \beta_i S) \), \( g(N, P) = N \sum_{i=1}^{n} \theta_i \alpha_i (1 - \exp(-a_i \beta_i S)) \), and \( S = \frac{P}{1 + \sum_{i=1}^{n} a_i b_i \alpha_i N} \).

Assume \((\alpha, \beta)\) is the coESS and \((\hat{N}, \hat{P})\) is the equilibrium achieved by the populations playing the coESS. By the Jury conditions, \((\hat{N}, \hat{P})\) is linearly stable if and only if

\[
2 > 1 + |D| > |T|
\]

where \( T \) and \( D \) denote the trace and determinant, respectively, of the Jacobian matrix

\[
\begin{bmatrix}
\frac{\partial f}{\partial N}(\hat{N}, \hat{P}) & \frac{\partial f}{\partial P}(\hat{N}, \hat{P}) \\
\frac{\partial g}{\partial N}(\hat{N}, \hat{P}) & \frac{\partial g}{\partial P}(\hat{N}, \hat{P})
\end{bmatrix}
\]

Using the facts that \( \sum_{i=1}^{n} \lambda_i \alpha_i \exp(-a_i \beta_i \hat{S}) = 1, \exp(-a_i \beta_i \hat{S}) = \frac{1}{\lambda_i} \), and \( \hat{P} = \sum_i \alpha_i \theta_i (1 - \exp(-a_i \beta_i \hat{S})) \), we get that

\[
\begin{align*}
\frac{\partial f}{\partial N}(\hat{N}, \hat{P}) &= 1 - \hat{N} \sum_i \alpha_i a_i b_i \frac{\partial S}{\partial N}(\hat{N}, \hat{P}) \\
\frac{\partial f}{\partial P}(\hat{N}, \hat{P}) &= -\hat{N} \sum_i \alpha_i a_i b_i \frac{\partial S}{\partial P}(\hat{N}, \hat{P}) \\
\frac{\partial g}{\partial N}(\hat{N}, \hat{P}) &= \frac{\hat{P}}{\hat{N}} + \hat{N} \sum_i \theta_i \alpha_i a_i b_i \frac{\partial S}{\partial N}(\hat{N}, \hat{P}) \\
\frac{\partial g}{\partial P}(\hat{N}, \hat{P}) &= \hat{N} \sum_i \theta_i \alpha_i a_i b_i \frac{\partial S}{\partial P}(\hat{N}, \hat{P})
\end{align*}
\]

Thus,

\[
T = 1 + \hat{N} \sum_i \alpha_i a_i b_i \left( \frac{\theta_i \frac{\partial S}{\partial P}}{\lambda_i} + \frac{\frac{\partial S}{\partial N}}{\hat{N}} \right)
\]

\[
D = \hat{N} \sum_i \alpha_i a_i b_i \left( \frac{\theta_i \frac{\partial S}{\partial P}}{\lambda_i} + \frac{\hat{P} \frac{\partial S}{\partial P}}{\hat{N}} \right)
\]

We have that

\[
\frac{\partial S}{\partial P}(\hat{N}, \hat{P}) = \frac{\hat{S}}{\hat{P}}
\]

Since \( 1 + \sum_i a_i b_i \alpha_i \hat{N} = \frac{\hat{P}}{\hat{S}} \), we get

\[
\frac{\partial S}{\partial N}(\hat{N}, \hat{P}) = -\frac{\hat{P} \sum_i a_i b_i \alpha_i}{\left(1 + \sum_i a_i b_i \alpha_i \hat{N}\right)^2} = -\frac{\hat{S}(\hat{P}/\hat{S} - 1)/\hat{N}}{\hat{P}/\hat{S}} = \frac{\hat{S}}{\hat{N}} \left( \frac{\hat{S}}{\hat{P} - 1} \right)
\]

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Hence, the trace and determinant expressions simplify to

\[ T = 1 + \hat{N} \sum_i \alpha_i \alpha_i \beta_i \left( \frac{\theta_i \hat{S}}{\lambda_i \hat{P}} + \frac{\hat{S}}{\hat{N}} \left( 1 - \frac{\hat{S}}{\hat{P}} \right) \right) \]

\[ D = \hat{N} \sum_i \alpha_i \alpha_i \beta_i \left( \frac{\theta_i \hat{S}}{\lambda_i \hat{P}} + \frac{\hat{S}}{\hat{N}} \right) \]

Since \( 1 - \frac{\hat{S}}{\hat{P}} < 1 \), it follows immediately that \( 1 + |D| > T \). Hence \((\hat{N}, \hat{P})\) is linearly stable if and only if

\[ \hat{N} \sum_i \alpha_i \alpha_i \beta_i \left( \frac{\theta_i \hat{S}}{\lambda_i \hat{P}} + \frac{\hat{S}}{\hat{N}} \right) < 1 \]

Equivalently, as \( \beta_i \hat{S} = \hat{S}_i = \frac{\ln \lambda_i}{\alpha_i} \),

\[ \sum_i \alpha_i \ln \lambda_i \left( \frac{\theta_i \hat{N}}{\lambda_i \hat{P}} + 1 \right) < 1 \]