A Mathematical Model of the Paradox of Enrichment in Arthropods: Comparison between Theory and Experiment

Abstract
The paradox of enrichment refers to a situation in which an originally stable predator-prey ecosystem is destabilized by tripling the food supply available to the herbivore, resulting in the extinction of both species due to overexploitation. An existing arthropod predator-prey model incorporating age structure in the carnivore is extended to include the effects of intraspecific carnivore competition. A linear stability analysis of the community equilibrium point of that differential-integral equation system is performed and the results are compared to those obtained by employing an analogous differential equation model without age structure. It is shown that, unlike for the latter model, the paradox of enrichment can now occur even for a carnivore which exhibits intraspecific carnivore competition. This prediction is in accordance with relevant experimental evidence involving mites on oranges.

Introduction
The paradox of enrichment is a term coined by University of Arizona ecologist M. L. Rosenzweig (1971) to describe the outcome of a laboratory experiment involving two mite species conducted by a team of Berkeley entomologists under the direction of C. B. Huffaker. The ecosystem under examination consisted of the herbivorous six-spotted spider mite Eotetranychus sexmaculatus Riley feeding on oranges while, in turn, being preyed upon by the carnivorous mite Metaseiulus occidentalis Nesbitt in a controlled environment of carefully constructed cabinets. Huffaker et al. (1963) observed that for universes composed of a particular fixed amount of oranges the population densities of the two mite species per cabinet tended to persist in ecological time. Then they were able to destabilize this originally stable situation by tripling the food supply available to the herbivorous mite, which resulted in the extinction of both mite species due to overexploitation. In what follows we shall survey two attempts to model this phenomenon mathematically.

The Differential Equation Model
Rosenzweig (1971) modeled this two-species ecosystem by introducing two differentiable functions, \( H(t) \) and \( C(t) \), which represented the population densities of herbivores (the prey) and carnivores (the predators) at time, \( t \). Assuming the occurrence of overlapping generations, he posed a series of differential equation models to describe the sizes of these populations. For our purposes it suffices to consider the generic system

\[
\frac{dH}{dt} = r(H)H - CF(H) = F(H,C)
\]  
(1a)

and

\[
\frac{dC}{dt} = -C - r_2(C,H)C = G(H,C)
\]  
(1b)
which preserves the essential features of Rosenzweig's analysis. Here \( r(H) \) is the intrinsic per capita growth rate of prey when no predators are present, \( f(H) \) is the functional response of the predator—i.e., the density of prey killed per unit time by a single average predator, \( r_2 \) is the maximum per capita intrinsic growth rate of the predator with an unlimited food supply, and \( g(H,C) \) represents the conversion of prey consumed into predator births. Implicit to the formulation of this system is the requirement that these populations must be relatively numerous and distributed uniformly in space. Note that in (1a) and (1b) we have chosen the time scale so that the lifetime of the predator is one unit—i.e., one unit of time \( = 16 \) days.

There exists a critical point \((H_0, C_0)\) of the system of (1)—i.e., a steady state solution

\[
H(t) = H_0 \quad \text{and} \quad C(t) = C_0,
\]

satisfying

\[
F(H_0, C_0) = 0 \quad \text{and} \quad G(H_0, C_0) = 0,
\]

which represents a community equilibrium point provided

\[
H_0 = g^{-1}(1/r_2) > 0 \quad \text{and} \quad C_0 = r(H_0)H_0/f(H_0) > 0
\]

where

\[
g^{-1} \text{ is the inverse function of } g(H) = g(H, C_0).
\]

Although there exist critical points of our system containing zero components, that type of equilibrium where both species are present is the one of primary biological interest within the context of the experiments of Huffaker et al. One of the simpler ways to represent the community equilibrium point of (2) graphically is to plot the isoclines of system (1) simultaneously on a two-dimensional graph in the \( H-C \) plane (Rosenweig and MacArthur 1963). The herbivore isocline is the locus of those \( H \) and \( C \) that satisfy the condition

\[
F(H, C) = 0
\]

while the carnivore isocline satisfies the companion condition

\[
G(H, C) = 0.
\]

The point of intersection of these two curves represents the community equilibrium point as depicted in Figure 1a. Although the functions contained in \( F \) and \( G \) need only have a generic form that yields isoclines of the shape indicated in that figure, there is also some merit in offering an explicit representation. Toward that end we take \( r(H) \), \( f(H) \), and \( g(H, C) \) of the form

\[
r(H) = r_1(1 - H/K), \quad f(H) = aH/(H + b_1), \quad \text{and}
\]

\[
g(H, C) = H/(H + b_2 + b_3C^2)
\]

where

\[
r_1, K, a > 0, \quad 0 < b_1 < K, \quad \text{and} \quad 0 < b_2 < (r_2 - 1)K \quad \text{for} \quad r_2 > 1.
\]

In order to determine conditions under which there can exist a stable community equilibrium point for this system, we first perform a linear perturbation analysis of the critical point of (2). Thus we consider a solution of system (1) of the form

\[
H(t) = H_0 + x(t), \quad C(t) = C_0 + y(t)
\]

where

\[
|x| << H_0 \quad \text{and} \quad |y| << C_0.
\]

Substituting (5) into the basic equations of (1), expanding \( F \) and \( G \) in Taylor series about \( H = H_0 \) and \( C = C_0 \), making use of (2b), and neglecting all nonlinear terms in
the perturbation quantities \( x(t) \) and \( y(t) \), we obtain the following set of perturbation equations:

\[
\frac{dx}{dt} = F_1(H_0, C_0)x + F_2(H_0, C_0)y 
\]

(6a)

and

\[
\frac{dy}{dt} = G_1(H_0, C_0)x + G_2(H_0, C_0)y, 
\]

(6b)

where partial derivatives with respect to \( H \) and \( C \) have been designated by subscripts "1" and "2", respectively. Implicit to a predator-prey interaction, or more generally to any exploitation interaction, are the inequalities \( F_2(H, C) < 0 \) and \( G_1(H, C) > 0 \). The prey isocline of (3a), \( F(H, C) = 0 \), can be solved for \( C = P(H) \) to obtain \( F[H, P(H)] = 0 \). Differentiating this with respect to \( H \) and evaluating the resultant condition at equilibrium yields the following form for the prey perturbation equation

\[
\frac{dx}{dt} = \alpha(k_1x - y), 
\]

(7a)

where \( \alpha = -F_2(H_0, C_0) > 0 \) and \( k_1 = P'(H_0) \). Similarly the predator isocline of (3b), \( G(H, C) = 0 \), can be solved for \( H = V(C) \) and then proceeding in an identical manner to that outlined above, the predator perturbation equation becomes

\[
\frac{dy}{dt} = \beta(x - k_2y) 
\]

(7b)

where \( \beta = G_2(H_0, C_0) > 0 \) and \( k_2 = V'(C_0) \).

We now look for solutions of (7) of the form

\[
[x, y]_t = [A, B]e^{\lambda t} 
\]

(8)

where \( \lambda \) is the growth rate of the perturbation quantities, while \( A \) and \( B \) are constants which could be determined given initial values for the perturbations. Substituting (8) into (7), we obtain two linear homogeneous equations in the two constants \( A \) and \( B \). If this eigenvalue system for \( \lambda \) is to have a nontrivial solution for the eigenvector components \( A \) and \( B \), then the determinant of their coefficients must vanish. That requirement

\[
\begin{vmatrix}
\alpha k_1 - \lambda & -\alpha \\
\beta & -\beta k_2 - \lambda
\end{vmatrix} = 0
\]

yields the following so-called secular equation for \( \lambda \):

\[
\lambda^2 + (\beta k_2 - \alpha k_1)\lambda + \alpha \beta (1 - k_2 k_1) = 0. 
\]

(9)

An interpretation of the parameters appearing in the above secular equation seems appropriate at this point. The exploitation parameters \( \alpha \) and \( \beta \) are a measure of the strength of the interspecific interactions at equilibrium, while \( k_1 \) and \( k_2 \) are related to the slopes of the isoclines at equilibrium and hence involve intraspecific interactions for the prey and predator, respectively. Intraspecific herbivore competition occurs when \( k_1 < 0 \) and herbivore mutualism, or cooperation, when \( k_1 > 0 \). For \( k_2 > 0 \) intraspecific carnivore competition results, while \( k_2 < 0 \) corresponds to carnivore mutualism. Should \( k_2 = 0 \), there is no intraspecific carnivore interaction. In particular for the functions defined in (4), the corresponding prey and predator isoclines are given by

\[
C = P(H) = \frac{r_1}{a} (H + b_1) (1 - H/K) \text{ for } 0 \leq H \leq K 
\]

(10a)

and

\[
H = V(C) = \frac{b_2 + b_3 c^2}{r_2 - 1} \text{ for } C \geq 0, 
\]

(10b)
respectively. We note that when $b_3 = 0$, the predator isocline reduces to the line
—i.e., no intraspecific carnivore interaction—originally treated by Rosenzweig (1971).
For intraspecific carnivore competition, $b_3 > 0$. Viewing $H$ as the independent variable
$H \equiv b_3/(r_2 - 1) < K$. Hence $k_2 = 0$ and this is the case of nonsquabbling predators
for both isoclines, $k_1$ and $1/k_3$ represent the slopes of the prey and predator isoclines,
respectively, at equilibrium in Figure 1a. That is, the predator isocline of (10b) would be given by
\[
C = \left[ \frac{(r_2 - 1)H - b_2}{b_3} \right]^{k_1} \quad \text{for } H \geq b_2/(r_2 - 1).
\] (10c)

Since
\[
\lim_{t \to -} e^{\lambda t} = \lim_{t \to +} e^{(Re\lambda)t} = \begin{cases} 
0 & \text{Re}\lambda < 0 \\
1 & \text{Re}\lambda = 0 \\
\infty & \text{Re}\lambda > 0 
\end{cases}
\] (11)
we say that the stability behavior of the solution of (1), given by the critical point of
(2), to perturbations of the type of (5) and (8) depends upon the sign of ReA with
stability occurring when ReA < 0 for all $\lambda$ satisfying (9). Equation (9) is of the form
\[
\lambda^2 + b\lambda + c = 0
\] (12a)
with
\[
b = \beta k_2 - \alpha k_1 \quad \text{and} \quad c = \alpha \beta (1 - k_2 k_1).
\] (12b)
Noting that such quadratics have roots $\lambda$ satisfying Re$\lambda < 0$ if and only if (Uspe\nsky 1948)
\[
b > 0 \quad \text{and} \quad c > 0,
\] (12c)
we have stability for those $k_2$ and $k_1$ such that
\[
k_1 < \frac{\beta}{\alpha} k_2 \quad \text{and} \quad k_1 k_2 < 1
\] (13)
since $\alpha \beta > 0$. This region can be represented graphically in the $k_2 - k_1$ plane as in
Figure 1b which has been drawn for $\alpha = \beta = 4.5$.

Rosenzweig (1971) considered exploitation in a two species ecosystem with a verti-
cal predator isocline ($k_3 = 0$) and with the prey limited by their environment to a
finite carrying capacity, $K$, which was an increasing function of their food supply. Observe from (13) or from an examination of the $k_1$ axis in Figure 1b that when $k_2 = 0
(b_3 = 0)$ there will be local stability of the community equilibrium point provided
\[
k_1 < 0.
\] (14)

Given the stability criterion of (14), Rosenzweig concluded that a predator-prey system
which originally had a prey carrying capacity $K_1$ corresponding to a $k_1 < 0$ could be
desitized by enriching the food source of the prey sufficiently so that the new carry-
ing capacity $K_2$ would correspond to a $k_1 > 0$ (see the vertical $b_3 = 0$ isocline of Fig.
1a). Since the predator density at equilibrium increased as the system was enriched
while the prey density remained the same by virtue of the vertical predator isocline,
Rosenzweig (1971) conjectured that the predator was relatively too numerous for the
prey at equilibrium for the system to persist. However, for intraspecific carnivore inter-
action of a competitive nature ($k_2 > 0$), Rosenzweig (1972) found that enrichment
inevitably resulted in a new stable ($k_1 < 0$) community equilibrium point with higher
population density levels for both species (see the $b_3 > 0$ isocline of Fig. 1a), since the
fourth quadrant of the $k_2 - k_1$ plane lies entirely within the stability region of Figure 1b.
As has just been demonstrated, the paradox of enrichment can occur for a differential equation model only when there is a vertical predator isocline. It is natural then to ask how this restriction compares with the experimental findings of Huffaker et al. (1963). In universes with the greater food supply the peak prey and predator densities averaged 2500 and 98, respectively, per cabinet as compared with the corresponding

![Figure 1](a) A schematic plot of the prey and predator isoclines relevant to the paradox of enrichment showing the effect of increasing the prey carrying capacity from $K_1$ to $K_2$ on the community equilibrium point (intersection of isoclines) for no intraspecific carnivore interaction (vertical line or $b_3 = 0$) and for intraspecific carnivore competition ($b_3 > 0$). For the experiments of Huffaker et al. (1965), $K_2 = 3K_1$ and the intersection points measured in number of mites per cabinet were (900, 17) and (2500, 98). (b) The stability region (shading) in the $k_2 - k_1$ for the differential equation model with values of the exploitation parameters $\alpha = \beta = 4.5$.  

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densities of 900 and 17 for the stable universes with one-third the food supply. Since
the predator to prey ratio more than doubled upon enrichment, the result was near annihilation of the prey through overexploitation. Observe that a vertical predator isocline which preserved the predator to prey ratio of the experimentally enriched system would have required an equilibrium point of 900 prey and 35 predators per cabinet. Hence the population density data for this experiment strongly suggests a nonvertical predator isocline of a competitive nature (see Fig. 1a). In order to devise a model that will predict the occurrence of a paradox enrichment in this instance, we now incorporate the effect of age structure, of a simple kind, in the predator population. We assume, for simplicity, that death in the predator comes only as a consequence of reaching a certain age which coincides with the normal ovipositional period. Then considering \( C(a,t) \) to be the population density of carnivores of age \( a \) at time \( t \), where we have chosen the same scale for age and time, the continuity-type age structure equation

\[
\frac{\partial C}{\partial t} + \frac{\partial C}{\partial a} = 0, \quad 0 < a < 1,
\]

holds. A boundary condition describing the birth rate

\[
\tilde{C}(0,t) = r_2[ g(H,C)C(t) ] = h(t)
\]

must be included. Finally our death rate assumption implies

\[
C(t) = \int_0^1 \tilde{C}(a,t) da.
\]

The von Foerster (1959) equation of (14) can be solved by the method of characteristics as follows. Beginning with (14), we introduce the characteristic coordinates \( \xi, \eta \) such that

\[
t = t(\xi, \eta) \quad \text{and} \quad a = a(\xi, \eta)
\]

where

\[
\frac{\partial t}{\partial \xi} = \frac{\partial a}{\partial \eta} = 1
\]

and

\[
t(\xi, 0) = \xi, \quad a(\xi, 0) = 0.
\]

Thus, from (14) and (17), we can deduce that

\[
C(\xi, \eta) = C[a(\xi, \eta), t(\xi, \eta)]
\]

satisfies

\[
\frac{\partial C}{\partial \xi} = 0
\]

and

\[
C(\xi, 0) = h(\xi).
\]

Solving (17) and (19), we find that

\[
t(\xi, \eta) = \xi + \eta, \quad a(\xi, \eta) = \eta, \quad \text{and} \quad C(\xi, \eta) = h(\xi).
\]

Now inverting the transformation of (16) and (18), we obtain

\[
\tilde{C}(a, t) = h(t - a).
\]

Then substitution of (21) into the relationship of (15) yields

\[
C(t) = \int_0^1 h(t - a) da.
\]
Finally, employing the change of variables
\[ s = t - a \]
in the integral on the right-hand side of (22), the following governing equation for \( C(t) \) results
\[ C(t) = \int_{t-1}^{t} r_2 g(H, C)(s) \, ds \]
upon introducing the explicit form of \( h(s) \) from (14b).

Our age structure model retains the differential equation (1a) for the prey but replaces (1b) with the integral equation (24). The construction of this model was inspired by earlier models (Wollkind and Logan 1978) of the predator-prey interaction between the McDaniel spider mite *Tetranychus mediini* McGregor, a pest on apple tree foliage, and its control agent, *M. occidentalis*, an ecosystem very much like the one studied by Huffaker et al. (1963). It is a generalization of an age structure model that was developed in (Hastings and Wollkind 1982). The community equilibrium point for the system consisting of (1a) and (24) is identical to that defined by (2). A linear perturbation analysis of that critical point for this age structure system can be shown to yield the following secular equation for \( \lambda \) (Smith and Wollkind 1983):
\[ \lambda - (1 - Bk_2)\kappa(\lambda) \lambda + \left[ ak_1 (1 - Bk_2) + \alpha B \kappa(\lambda) - ak_1 \right] = 0 \]  
where
\[ \kappa(\lambda) = \begin{cases} (1 - e^{-\lambda})/\lambda & \lambda \neq 0 \\ 1 & \lambda = 0 \end{cases} \]
while the parameters appearing in (25a) are to be interpreted just as they were earlier. The stability behavior of this quasi-polynomial secular equation has recently been investigated (Smith and Wollkind 1983). We summarize the results of that analysis for the case of \( a = \beta = 4.5 \), or more generally when \( a\beta > 2\pi^2 \), corresponding to the conditions for which Figure 1b was drawn. The stability region in that instance \( (a\beta > 2\pi^2) \) is bounded by the portion of the hyperbola
\[ \frac{\beta}{\alpha} = \text{for } k_1 \leq -2\sqrt{\frac{\beta}{\alpha}} \]
and a curve given parametrically by
\[ k_2 = \frac{1}{\beta} \left[ 1 - \frac{1}{2} \left( \frac{\beta}{1 - \cos \theta} - ak_1 \right) \right], \]
\[ k_1 = -\sqrt{2a\beta - \theta^2} \quad \text{for } 0 < \theta < 2\pi \]
as depicted in Figure 2.

Upon examination of this figure in comparison with Figure 1, we see that the destabilizing effect of age structure now makes it possible to extend the paradox of enrichment to the case of \( k_2 > 0 \). We first observe from Figure 1a that enriching an originally stable ecosystem involving intraspecific carnivore competition will most likely result in a new equilibrium point for which both \( k_1 < 0 \) and \( k_2 > 0 \) have been increased.

For \( a\beta > 2\pi^2 \) there can be instability for any \( k_2 \) provided \( k_1 > \sqrt{\frac{2\alpha\beta - 4\pi^2}{\alpha}} \), which is the horizontal asymptote in Figure 2. Hence, given the behavior of \( k_1 \) and \( k_2 \) with enrichment mentioned above, our age structure model admits the possibility of the paradox of enrichment occurring even in the presence of intraspecific carnivore compe-
Figure 2. The stability region (shading) in the $k_1 - k_2$ plane for the age structure model with $\alpha = \beta = 4.5$.

...tion, and that possibility becomes greater as the parameter $\alpha\beta$, a measure of interspecific interaction, increases. This phenomenon is in accordance with the experimental work of Huffaker et al. (1963). Thus the differential equation model without age structure does not predict the occurrence of a paradox of enrichment in this instance, whereas such a prediction is consistent with the stability results of our age structure model.

Validation procedures of this sort are the last step in any example of comprehensive applied mathematics. The latter involves taking some real world phenomenon, modeling it mathematically, and thereby making theoretical predictions which are then tested against observables of the phenomenon. The higher this correlation is, the better the model is judged to be. In other words, the proof of such an applied mathematics pudding is in the eating.

Literature Cited


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