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PREDATOR–PREY SYSTEMS WITH GROUP DEFENCE: THE PARADOX OF ENRICHMENT REVISITED

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The main concern of this paper is with survival or extinction of predators in models of predator–prey systems exhibiting group defence of the prey. It is shown that if there is no mutual interference among predators, enrichment could result in their extinction. However, if there is mutual interference, the predator population survives (at least deterministically).

1. Introduction. In a well-known and controversial paper, Rosenzweig (1971) warns that "Man must be careful in attempting to enrich ecosystems in order to increase its food yield. There is a real chance that such activity may result in a decimation of the food species that are wanted in greater abundance." He considers six different mathematical models of predator–prey (or parasite–host) interaction and shows that sufficient enrichment or increase of the prey-carrying capacity can cause destabilization of an otherwise stable interior equilibrium. Using a truncation for the sake of biological reality he also integrates the equations numerically and obtains extinction of the predator.

Several authors including Gilpin (1972), May (1972) and Riebesell (1974) criticize Rosenzweig's predictions. They show that the destabilization of the equilibrium results in the birth of an asymptotically stable periodic orbit. Freedman (1976, 1980) shows that for a class of generalized Gause models of predator–prey interaction this destabilization of the equilibrium is due to

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a Hopf bifurcation. Most of the models that Rosenzweig (1971) considered are special cases of models in this class. Rosenzweig (1972a,b) defends his conclusions by pointing out that if the amplitude of the periodic orbit is sufficiently large, sections of it may become dangerously close to one or both of the coordinate axes. It might therefore be very likely that some random perturbation (of even a minor nature) could result in the extinction of one or both populations.

McAllister *et al.* (1972) criticize Rosenzweig's warning by giving experimental evidence that shows moderate enrichment can be beneficial. However, there is exerimental evidence that seems to indicate that in some situations Rosenzweig's warning is valid. For example Huffaker *et al.* (1963) were able to obtain destabilization and extinction of an otherwise stable exploitation system involving an acrophagous mite (exploiter) and herbivorous mite (victim) by trebling the food density of the victim. Luckinbill (1973) and Schaffer and Rosenzweig (1978) were also able to find evidence connecting enrichment to dynamic instability.

It is the purpose of this paper to provide more support for Rosenzweig's warning, although for different reasons. In most predator–prey models considered in the literature, the predator response to prey density is assumed to be monotonic increasing (Holling 1965), the inherent assumption being that the more prey in the environment, the better off the predator. However, there is experimental and observational evidence that indicates that this need not always be the case, for example in the case of 'group defence.'

Group defence is a term used to describe the phenomenon whereby predation is decreased, or even prevented altogether, due to the increased ability of the prey to better defend or disguise themselves when their numbers are large enough. An example of this phenomenon is described by Tener (1965). Lone musk ox can be successfully attacked by wolves. Small herds of musk ox (2–6 animals) are attacked but with rare success. No successful attacks have been observed in larger herds. A second example described by Holmes and Bethel (1972) involves certain insect populations. Apparently, large swarms of the insects make individual identification difficult for their predators.

Related examples of non-monotone consumption occur at the microbial level where there is considerable evidence (Andrews, 1968; Aris and Humphrey, 1977; Boon and Laudelout, 1962; Bush and Cook, 1976; Yang and Humphrey, 1975), which indicates that when faced with an overabundance of nutrient the effectiveness of the consumer can begin to decline. That is, certain nutrients may be growth-limiting at low concentrations as well as growth-inhibiting at high concentrations. This is often seen when micro-organisms are used for waste decomposition or for water purification.

This phenomenon is called 'inhibition' of the consumer by high densities of the resource.

With the phenomenon of group defence in mind it is therefore of interest to study mathematical models of predator–prey interactions in which the predator response function is not necessarily a monotone increasing function of prey density, but rather is only monotone increasing until some critical density and then becomes monotone decreasing. We are unaware of literature reports of predator–prey models incorporating such non-monotone functional responses.

In Section 2 of this paper we re-examine the paradox of enrichment in the light of group defence. We show that enrichment can, indeed, lead to extinction in a closed ecosystem as originally postulated by Rosenzweig (1971). However, just as in Rosenzweig's original paper we draw the conclusion only if we assume that "the exploiters do not actually interfere with each other". In Section 3 we incorporate mutual interference of the predators in the model as was done in Erbe and Freedman (1985), Freedman (1979) and Freedman and Rao (1983). See also Beddington (1975), Hassell (1971) and Rogers and Hassell (1974). Just as in the previous work mentioned we find that mutual interference is stabilizing (at least deterministically). However, we observe by means of a series of numerical examples that, viewed stochastically, there might be a larger probability that the predator population may become extinct as mutual interference becomes stronger and stronger. We conclude with a discussion in Section 4.

2. *Group Defence—No Mutual Interference.*

We propose the following system of autonomous ordinary differential equations of generalized Gause-type as a model of predator–prey interaction with group defence exhibited by the predator

$$\begin{gathered} \dot{x}=xg(x,K)-yp(x) \\ \dot{y}=y(-s+q(x)) \\ x(0)\geq 0,\ y(0)\geq 0,\ {}^{\boldsymbol{\cdot}}=\tfrac{d}{dt} \end{gathered} \tag{1}$$

where $x(t)$ and $y(t)$ denote the density of prey and predator, respectively. We assume that the functions g, p and q are continuously differentiable and that s and K are positive constants.

Here, $g(x,K)$ represents the specific growth rate of the prey in the absence of predation and is assumed to satisfy

$$\begin{gathered} g(0,K)>0,\ g(K,K)=0,\ g_x(K,K)<0 \\ g_x(x,K)\leq 0 \text{ and } g_K(x,K)>0 \text{ for any } x>0. \end{gathered} \tag{2}$$

The function $p(x)$ denotes the predator response function. We assume $p(x)$ satisfies

$$p(0)=0,\ p(x)>0 \text{ for } x>0 \tag{3}$$

and that there exists $M>0$ such that

$$p'(x)>0 \text{ for } 0\leq x<M.$$

and

$$p'(x)<0 \text{ for } x>M.$$

The rate of conversion of prey to predator is described by $q(x)$. In Gause's model $q(x)=cp(x)$ for some positive constant c. We assume $q(x)$ has properties similar to $p(x)$. In particular

$$q(0)=0,\ q(x)>0 \text{ for } x>0,\ q(M)>s$$

$$q'(x)>0 \text{ for } 0\leqslant x<M \tag{4}$$

and

$$q'(x)<0 \text{ for } x>M.$$

Specific examples of $g(x,K)$, $p(x)$ and $q(x)$ can be found in Boon and Luadelout (1962), Holling (1965), May (1972), Rosenzweig (1971), and Yang and Humphrey (1975).

The existence of $M>0$ is precisely the assumption which models group defence. It is also only reasonable to assume that the same M holds for both p and q since the conversion of prey to predator should increase and decrease as the consumption of prey increases and decreases. We assume that $q(M)>s$ since otherwise the predator cannot survive on the prey at any density. Therefore, there exists $\lambda<M$ such that $q(\lambda)=s$ and there may exist $\mu>M$ such that $q(\mu)=s$. We assume that $\lambda<K$ or again the predator cannot survive on the prey.

From the above assumptions one can conclude that there is always an interior equilibrium, E_λ, of the form $(\lambda,\lambda g(\lambda,K)/p(\lambda))$ where $q(\lambda)=s$, $p'(\lambda)>0$ and $q'(\lambda)>0$. Furthermore, it follows from a standard linear analysis (see Freedman 1976, 1980) that this equilibrium is stable or unstable according to whether the slope of the prey isocline at E_λ is negative or positive.

Our first observation follows as in Freedman (1976, 1980) (see Figs 1 and 2).

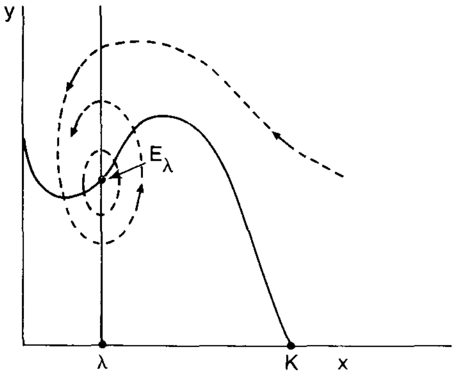

Figure 1. Predator–prey dynamics for (1) in the case $q(x)>s$ for $x>M$: ——— isoclines; — — — orbits.

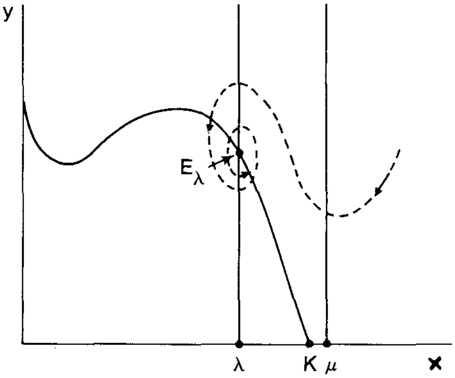

Figure 2. Predator–prey dynamics for (1) in the case $\lambda<K<\mu$: ——— isoclines; — — — orbit.

THEOREM 1. *If*

$$\lim_{x\to\infty} q(x) \geqslant s \tag{5}$$

(*i.e. no* $\mu>M$ *exists such that* $q(\mu)=s$) *or if* $q(\mu)=s$ *where* $\lambda<K>\mu$, *then solutions of* (1) *with positive initial conditions either approach* E_λ *or approach a positive limit cycle surrounding* E_λ *or are themselves periodic solutions surrounding* E_λ.

If on the other hand $\mu<K$, the dynamics differ substantially (see Figs 3a–c). In particular, for a significant set of initial conditions the predator can be driven to extinction (see Figs 3 and 4).

The variational matrix about any equilibrium (x^*,y^*) is:

$$V(x^*,y^*)=\begin{bmatrix} x^*g_x(x^*,K)+g(x^*,K)-y^*p'(x^*) & -p(x^*) \\ y^*q'(x^*) & -s+q(x^*) \end{bmatrix}. \tag{6}$$

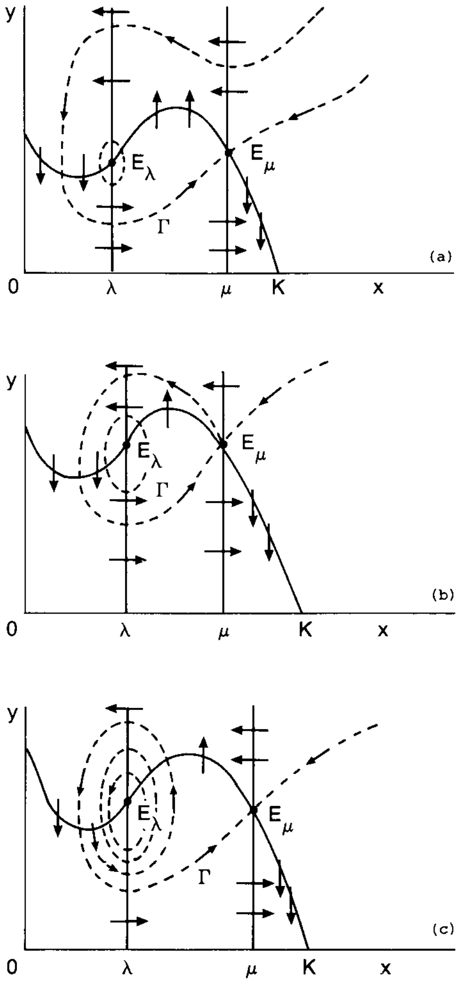

Figure 3. Predator–prey dynamics for (1) in the case $\lambda<\mu<K$: ——— isoclines; — — — — — $W^s(E_\mu)$; —·—·— periodic orbit(s) surrounding E_λ. (a) Γ comes from $x(t)>\mu$. Solutions starting outside the region bounded by $W^s(E_\mu)$ converge to E_K. (b) Γ is a homoclinic orbit. The only solutions that do not converge to E_K originate inside the region bounded by Γ or lie on $W^s(E_\mu)$. (c) Γ satisfies $x(t)<\mu$ for all t. The only solutions that do not approach E_K are those that lie on $W^s(E_\mu)$ or those originating inside the outermost periodic orbit (if one exists).

At $(x^*,y^*)=(K,0)$ this becomes

$$V(K,0)=\begin{bmatrix} Kg_x(K,K) & -p(K) \\ 0 & -s+q+(K) \end{bmatrix} \tag{7}$$

and so both eigenvalues are negative. Therefore, the equilibrium $E_K=(K,0)$ is locally asymptotically stable which implies that there is a set of initial conditions of positive measure in the interior of the positive cone for which

$$\lim_{t\to\infty} y(t)=0.$$

Also, in the case $\mu<K$, there exists a second interior equilibrium $E_\mu=(\mu,\mu g(\mu,K)/p(\mu))$.

$$V(E_\mu)=V(\mu,y)= \begin{bmatrix} \mu g_x(\mu,K)+g(\mu,K)-y^*p'(\mu) & -p(\mu) \\ y^*q'(\mu) & 0 \end{bmatrix}. \tag{8}$$

The constant term in the characteristic equation is therefore equal to $y^*q'(\mu)p(\mu)<0$ since $q'(\mu)<0$. Therefore, E_μ is always a saddle point. Observing the direction the solutions must cross the predator and prey isoclines one observes that there cannot be a periodic orbit surrounding E_μ (see Figs 3a–c).

Since E_μ is a saddle point, it has a one-dimensional stable manifold, $W^s(E_\mu)$ and hence there are two orbits that approach E_μ asymptotically. Consider the orbit that approaches E_μ from the left and call it Γ. There are at most three possibilities (see Figs 3a–c). Case 1: in negative time Γ can leave the strip $0\leq x\leq\mu$ (Fig. 3a). In this case all solutions with positive initial conditions that start outside the region bounded by $W^s(E_\mu)$ approach E_K asymptotically. Case 2: secondly, Γ can be a homoclinic orbit, that is tends to E_μ in negative time (Fig. 3b). In this case the only solutions with positive initial conditions that do not approach E_K originate inside the region bounded by Γ or on $W^s(E_\mu)$. Case 3: finally, Γ can remain in the strip $0\leq x<\mu$ for all backward time. In this case E_λ is either unstable with no periodic orbit surrounding it or it must be surrounded by one or more periodic orbits and the outermost one must be unstable from the outside. Γ then either approaches E_λ (in the case of no periodic orbit surrounding E_λ) or the outermost periodic orbit if time is followed in reverse. The only solutions that do not approach E_K are those that lie on $W^s(E_\mu)$ or those originating inside the outermost periodic orbit (if one exists).

Since enrichment results in an increase of the carrying capacity K, it is now easy to see that our model predicts that sufficient enrichment could result in extinction of the predator if the prey practice group defence. Consider model (1) with $K<\mu$. Then E_K is unstable and at least deterministically both populations persist uniformly (see Butler *et al.*, 1986). In fact, all solutions approach E_λ or some periodic orbit surrounding E_λ. At $K=\mu$, there is a bifurcation of the critical point E_K. As K increases beyond μ, E_K becomes asymptotically stable and E_μ appears in the interior of the non-negative cone. Thus there is a set of initial conditions of positive measure for which extinction of the predator results and so Rsenweig's warning applies. It is interesting to note that these outcomes are independent of the local stability of E_λ and hence of which side of the prey isocline E_λ lies on. Rather they depend upon whether or not $\mu<K$ and hence on whether or not E_μ lies on the positive cone.

In the following numerical example we see that as the carrying capacity K increases, the model exhibits the dynamics described in each of the three cases described above. Consider

$$\begin{aligned}\dot{x}&=2x(1-\frac{x}{K})-\frac{9xy}{x^2+3.35x+13.5}\\ \dot{x}&=y(-1+\frac{11.3x}{x^2+3.35x+13.5}).\end{aligned}\tag{9}$$

The functions and the values of the parameter have been chosen solely for convenience and have no biological significance. In Fig. 4a we see how increasing K affects the prey isocline. When $K=4$, then $\lambda<K<\mu$, and since the slope of the prey isocline is negative at E_λ^4, then E_λ^4 is asymptotically stable. (The superscripts differentiate the critical points for $K=4$ from those for $K=6$ or $K=7$.) If enrichment causes K to increase to $K=6$ (see Fig. 4b) we see that we are in Case 1. In this example, E_λ^6 is unstable and there is a unique asymptotically stable periodic orbit surrounding it. At $K=7$ (see Fig. 4c), we are in Case 3 (with no periodic orbit surrounding E_λ^7). Therefore, there must be some critical value K^*, $6<K^*<7$ for which the periodic orbit coalesces with a homoclinic orbit that is stable from within and unstable from without (i.e. Case 2).

This example illustrates that a sudden enrichment of a stable system could result in extinction of the predator. Let us assume that before enrichment ($K=4$) the predator–prey population densities stabilized near E_λ^4. Enriching this sytem to $K=6$ would probably not cause extinction since the point $E_\lambda{}^4$ is within the region of attraction of the stable periodic orbit surrounding $E_\lambda{}^6$. However, enriching the system further, to $K=7$, would

Figure 4. Predator–prey dynamics for example (9). (a) ——— isoclines. As K is increased from 4 to 6 to 7 the predator isoclines (the vertical lines $x=\lambda=2.45822$ and $x=\mu=5.49178$) remain unchanged. However, the prey isocline increases as K increases. ■ denotes E_λ^4, ○, ●, denote E_λ^4 and E_μ^4, respectively, and △, □ denote E_λ^7 and E_μ^7, respectively. (b) ——— isoclines, — — — — solutions starting close to E_μ^6 and spiralling out to a periodic orbit. Solutions which initiate inside the region bounded by $W^s(E_\mu^6)$ converge to the periodic orbit surrounding E_μ^6. Solutions initiating outside E_μ^6 converge to E_K^6. (c) ——— isoclines, — — — — solution starting close to E_λ^6. All solutions with positive initial conditions converge to E_K^6 except the solution E_λ^6 and solutions initiating on $W^s(E_\mu^6)$.

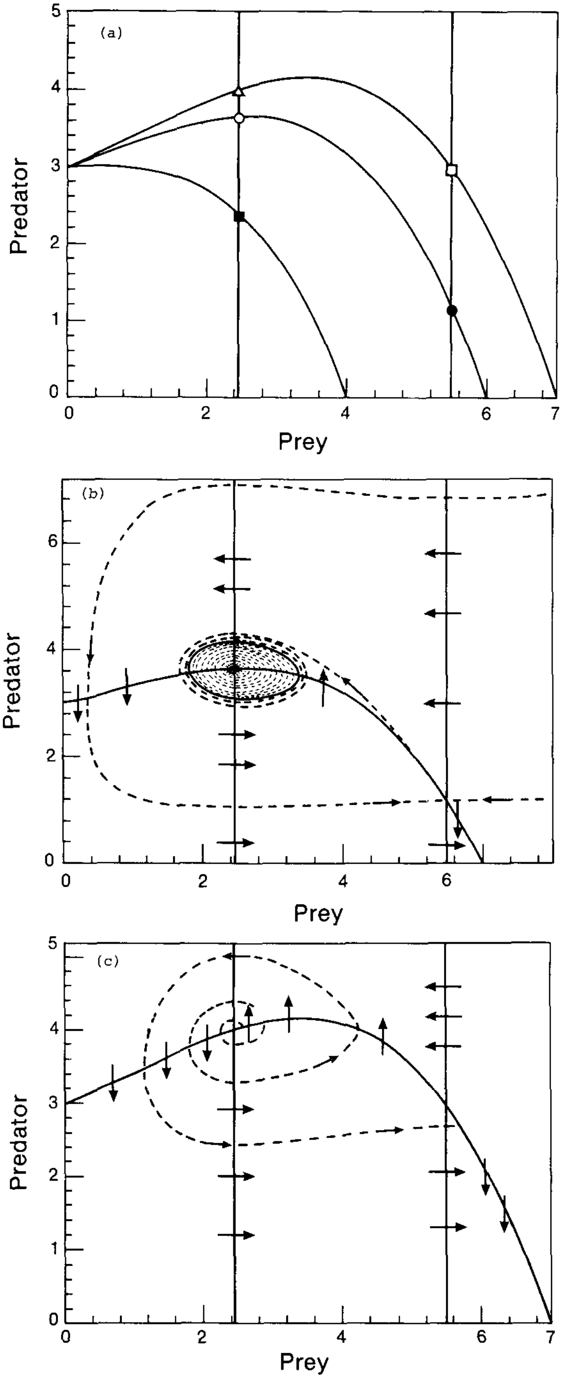
(a)
Predator
Prey
0
1
2
3
4
5
0
2
4
6
7
(b)
Predator
Prey
0
2
4
6
0
2
4
6
(c)
Predator
Prey
0
1
2
3
4
5
0
2
4
6
7

Figure 4.

most likely cause the extinction of the predator. (In fact, almost all initial conditions with $K=7$ result in extinction of the predator.) Thus enrichment could cause an otherwise stable ecosystem, one that had even reached steady state, to crash.

3. Group Defence Model with Mutual Interference. We now incorporate mutual interference in our model and write it in the form

$$\begin{aligned} \dot{x} &= xg(x,K) - y^m p(x) \\ \dot{y} &= -sy + y^m q(x) \\ x(0) &\geq 0,\ y(0) \geq 0 \end{aligned} \tag{10}$$

where $0<m<1$. Hence m denotes the mutual interference constant. All assumptions on the functions g, p and q are as in Section 2. The positive equilibria of this model are given by the intersection of the curves representing the predator and prey isoclines:

$$\begin{aligned} y^{1-m} &= q(x)/s \\ y^m &= \frac{xg(x,K)}{p(x)}. \end{aligned} \tag{11}$$

There is always at least one such equilibrium. Several examples are given in Figs 5a–c. In previous work (Freedman, 1979; Freedman and Rao, 1983), for a model without group defence, it was shown that mutual interference has a stabilizing influence on the positive equilibria of predator–prey systems. The same is true in the case of group defence. However, we are more interested in the global behaviour of our model. We show that all solutions of (10) initiating in the positive cone are eventually uniformly bounded away from the coordinate axes and hence both populations persist uniformly (at least deterministically). This enables us to conclude, though ‘with reservation’ that mutual interference is stabilizing.

We point out that (10) is not a dynamical system due to the sublinearity with respect to y which leads to non-uniqueness of solutions along the x-axis. However, if we restrict $y>0$ in (10), it is a dynamical system and uniqueness of solutions does hold.

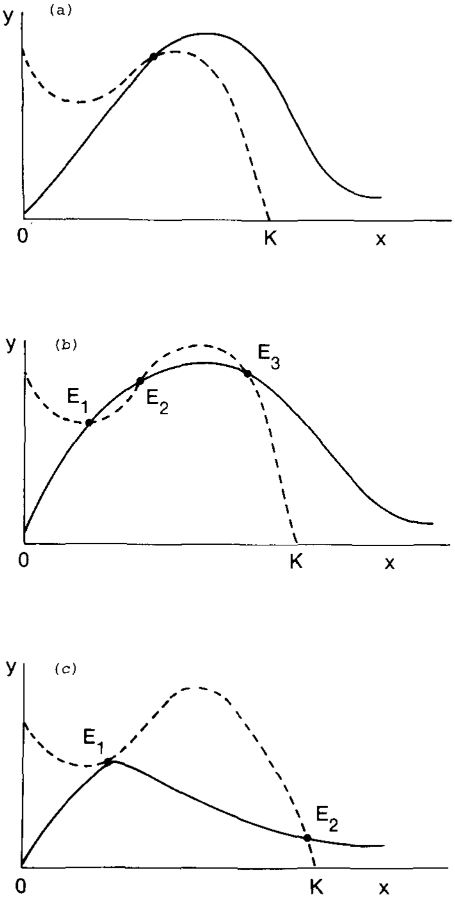

Figure 5. Predator–prey dynamics for (10). ——— predator isocline, — — — — prey isocline. (a) Isoclines intersect at only one point, E. (b) Isoclines intersect at three points, E_1, E_2, E_3. (c) Isoclines intersect at two points, E_1 and E_2.

THEOREM 2. *There exists* $\varepsilon>0$ *such that for all solutions of* (10) *with positive initial conditions,*

$$\liminf_{t\to\infty} x(t)\geq\varepsilon \text{ and } \liminf_{t\to\infty} y(x)\geq\varepsilon.$$

Thus, (10) is uniformly persistent.

Proof. (Understanding of the proof will be assisted by referring to Fig. 6. However, the proof does not depend on the particular configuration of the isoclines depicted in Fig. 6.)

Let c_1 denote the predator isocline and c_2 the prey isocline. Since there is at least one interior equilibrium, let $E_L=(x_L,y_L)$ denote the positive equilibrium with the smallest x coordinate. Let

$$\bar{M}=\max_{x\in[\frac{x_L}{2},K]}\left[\frac{xg(x,K)}{p(x)}\right]^{\frac{1}{m}} \tag{12}$$

and select

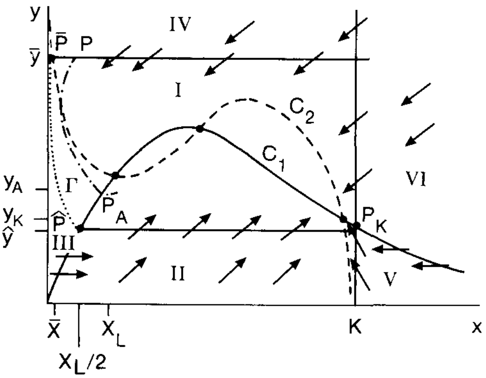

Figure 6. Predator–prey dynamics for (10). ——— predator isocline, c_1; — — — — — prey isocline, c_2. . . . . solution segment from $\bar{P}$ to $\hat{P}$, Γ. Regions I–VI are defined in the proof of Theorem 2. All solutions with positive initial conditions enter Region I in finite time and then remain there.

$$\bar{y}>\max\{\bar{M},\ [q(M)/s]^{\frac{1}{(m-1)}}\}. \tag{13}$$

(Recall that M was defined so that $q'(x)>0$ if $x<M$ and $q'(x)<0$ if $x>M$.) Let $P_K=(K,y_K)$ denote the point of intersection of c_1 with the vertical line $x=K$. Note $y_K>0$.

Consider the solution of (10) with initial condition $P=(x_L/2,\ \bar{y})$. By the definition of $\bar{y}$ it follows that for the solution through this point both $\dot{x}<0$ and $\dot{y}<0$. This solution must first cross c_2 vertically. Then x starts to increase while y continues to decrease until the solution crosses c_1 horizontally. Call this point of intersection $P_A=(x_A,y_A)$. If $y_A\geq y_K$, select any point $\hat{p}=(\hat{x},\hat{y})$ on c_1 with $\hat{x}<x_A$ and $\hat{y}<y_K$. If $y_A<y_K$ *let* $\hat{P}=P_A$. Follow the solution through $\hat{P}$ backward in time. By uniqueness of solutions it must cross the line $y=\bar{y}$ at some point $\bar{P}=(\bar{x},\bar{y})$ with $\bar{x}\leq x_L/2$. Call the solution curve from $\bar{P}$ to $\hat{P}$, r. Define

Region I = $\{(x,y)$: $\hat{y}\leq y\leq\bar{y}$, $x\leq k$ and x lies to the right of $\Gamma\}$.
Region II = $\{(x,y)$: $0\leq y\leq\hat{y}$, $x\leq K$ and x lies to the right of $c_1\}$.
Region III = $\{(x,y)$: $y<\bar{y}$, $x>0$, y lies above c_1 and x lies to the left of $\Gamma\}$.

Region IV = $\{(x,y)$: $0<x\leq K$, $y>\bar{y}\}$.
Region V = $\{(x,y)$: $x>K$, $y>0$ and y lies below $c_1\}$.
Region VI = $\{(x,y)$: $x\geq K$ and x lies above $c_1\}$.

It is easy to see that Region I is positively invariant and by the Poincare–Bendixson Theorem all solutions with positive initial conditions eventually enter Region I in finite time. The following directed graph shows all the possible routes solutions can take before they enter Region I

$$\begin{tikzcd}
 & \mathrm{IV} \arrow[ddl] \arrow[dd] & \\
 & & \mathrm{VI} \arrow[ul] \arrow[dl] \arrow[dd] \\
\mathrm{III} \arrow[ddr] & \mathrm{I} & \\
 & & \mathrm{V} \arrow[ul] \arrow[dl] \\
 & \mathrm{II} \arrow[uu] &
\end{tikzcd} \tag{14}$$

In Region III, once a solution is to the left of c_2, $\dot{x}>0$ and so it is not possible to converge to (0,0), but rather the solution must eventually cross c_1 into Region II. In Region II $\dot{y}>0$. Therefore the sublinearity with respect to y in (10) is not a problem in our analysis and the proof is complete. ■

Although we have shown that solutions are uniformly asymptotically bounded away from the axes, we do not claim that before entering Region I some solutions do not become dangerously close to one of the axes. A stochastic effect could then drive a population to extinction. However, this is also true before enrichment and/or when there is no mutual interference.

The following numerical example shows another reason why our conclusion that mutual interference is stabilizing is 'with reservation'. We consider the same example as in the previous section, after enrichment [i.e. model (9) with $K=7$]. This time we also incorporate mutual interference in the model. Consider

$$\begin{aligned}
\dot{x}&=2x\left(1-\frac{x}{7}\right)-\frac{9\,y^m x}{x^2+3.35x+13.5}\\
\dot{y}&=-y+\frac{11.3xy^m}{x^2+3.35x+13.5}.
\end{aligned} \tag{15}$$

We plot the predator and prey isoclines in Figs 7a–c for $m=0.95$, 0.75 and 0.5, respectively. In each case, there is only one interior equilibrium, E, and the density of the predator at E is dangerously small. Even though deterministically all populations survive, again a stochastic effect could conceivably result in the extinction of the predator since all solutions with positive initial conditions converge either to E or to a periodic orbit surrounding E, if one exists.

4. Discussion. In this paper we consider a predator–prey model in which the prey exhibit group defence. Such a model may be applicable in the case of animals such as musk ox that are better able to defend themselves against predators when in groups or in the case of insects where individual identification of the prey by the predator is a prerequisite to successful predation.

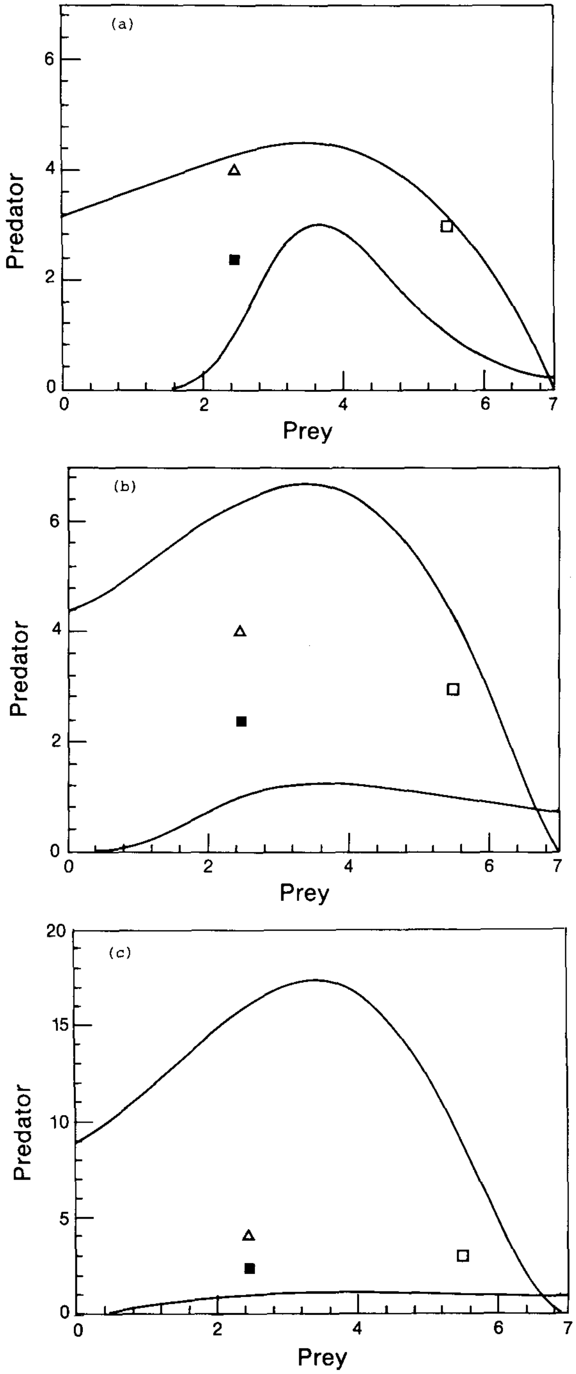

Figure 7. Predator–prey dynamics for (15). ——— predator and prey isoclines. ■, △, □ designate E^4_λ, E^7_λ and E^7_μ, respectively, for model (9). In (a) $m=0.95$, (b) $m=0.75$ and (c) $m=0.5$. In all cases the predator density at the unique interior equilibrium is very small and so the predator is in danger of extinction.

In the case where there is no mutual interference among hunting predators, our model predicts that group defence combined with sufficient enrichment can cause the predator population to become extinct. Thus we provide more support that Rosensweig's (1971) warning is valid, though for a significantly different reason.

If the predator exhibits mutual interference in seeking out prey, extinction due to group defence combined with enrichment may be averted. However, this conclusion is based solely on deterministic evidence. If stochastic effects were to be introduced, this conclusion would probably not be robust.

Of course, our models suppose a closed environment, whereas in the field extinction could be avoided by the predator seeking an alternative prey. McAllister *et al.* (1972) also mention that prey refuges, aestivation, resting stages, inhomogeneous distributions, fluctuating environmental conditions, or even man's harvesting might protect the predator population and Rosenzweig and Schaffer (1978) show that coevolutionary response to ecosystem enrichment enhances ecosystem stability.

We are grateful to John Holmes for supplying us with some of the references and to Michael Rosenzweig for a stimulating discussion over lunch.

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