Bifurcation Analysis of a Predator-Prey System Involving Group Defence

G. S. K. Wolkowicz

BIFURCATION ANALYSIS OF A PREDATOR-PREY SYSTEM INVOLVING GROUP DEFENCE*

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Abstract. A class of ODEs of generalized Gause type modeling predator-prey interaction is considered. The prey are assumed to exhibit a phenomenon called group defence, that is, predation is decreased or even eliminated due to the ability of the prey to defend or disguise themselves as their numbers increase.

Using the carrying capacity of the environment as the bifurcation parameter, it is shown that the model undergoes a sequence of bifurcations that includes a homoclinic bifurcation as well as a Hopf bifurcation. Conditions (that hold even in the case of no group defence) that ensure a subcritical Hopf bifurcation and also the spontaneous appearance of a semistable periodic orbit that splits into a pair (one stable and one unstable) of periodic orbits are given.

Ecological ramifications are considered. Unlike the classical model, sufficient enrichment of the environment combined with group defence leads to extinction of the predator (deterministically) for almost all initial conditions, providing strong support for the so-called "paradox of enrichment."

Key words. Hopf bifurcation, homoclinic bifurcation, semistable periodic orbit, predator-prey system, group defence

AMS(MOS) subject classifications. 92A15, 92A17, 34C15, 34C35

1. Introduction. In [10], Freedman and Wolkowicz introduce a model of predator-prey interactions in which the prey exhibit group defence. Group defence is a term used to describe the phenomenon whereby predation is decreased or even prevented altogether due to the ability of the prey to better defend or disguise themselves when their numbers are large. See Tener [26] and Holmes and Bethel [13] for examples where this phenomenon is known to occur in nature.

The model in [10] differs from the classical generalized Gause-type models of predator-prey interactions (see Freedman [9]) since in order to model group defence, the predator response function is no longer restricted to be a monotone increasing function of prey density. Rather, it increases until some critical density is reached and then decreases.

Freedman and Wolkowicz interpret the results of their analysis as evidence that one must heed the warning given by Rosenzweig in [22]:

> 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

the so-called paradox of enrichment (see also [10], [11], [18], [19], [21]–[24]). There is also experimental evidence supporting Rosenzweig's warning (see Huffaker et al. [15], Luckinbill [16], and Schaffer and Rosenzweig [25] for example).

In this paper a more complete global analysis of the model introduced in [10] is given. In [10] it was shown that for sufficient enrichment there is always a set of initial conditions of positive measure for which extinction of the predator results. This is strengthened in Theorem 3.7 where it is shown that there is actually a threshold of enrichment above which extinction of the predator results for all but a set of initial

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conditions of measure zero unless (see Proposition 3.8) the prey isocline is monotone decreasing for all values of the carrying capacity. In that case there is a separatrix. For all solutions initiating on one side of the separatrix, extinction of the predator results. Solutions initiating on the other side of the separatrix converge to an interior equilibrium. This contrasts with the dynamics of the classical model, where no group defence is assumed, since in that model the predator would never become extinct if the model is interpreted solely deterministically.

In [10], a numerical example is given indicating a sequence of bifurcations as the carrying capacity of the environment is increased. In particular, besides the exchange of stability between certain critical points, the example given in [10] undergoes a supercritical Hopf bifurcation as well as a stable homoclinic bifurcation. In this paper, it is shown that such a sequence of bifurcations, involving a homoclinic orbit for some critical value of the carrying capacity as well as a Hopf bifurcation, is a prototype and always occurs (unless the prey isocline is monotonically decreasing for all values of the carrying capacity). However, the order of the bifurcations need not be the same as in this example. The homoclinic bifurcation can be unstable rather than stable and the Hopf bifurcation can be subcritical rather than supercritical. In fact, we also show that even the classical model (that is, no group defence assumed), can undergo a subcritical rather than supercritical (as is usually considered) Hopf bifurcation.

The dynamics are reminiscent of the dynamics of the predator-prey system studied by Conway and Smoller in [6] where they assume the prey to be "asocial."

This paper is organized as follows. The predator-prey model is described in § 2, where properties of the isoclines are also derived. Preliminary analytic results appear in § 3 and the bifurcation analysis appears in § 4 where we describe the possible sequences of bifurcations and prove that there is always a homoclinic bifurcation (provided the prey isocline is not monotone decreasing for all values of the carrying capacity). A discussion of the implications of the results is given in § 5. For completeness the information obtained from a linear analysis is found in Appendix A and an example justifying certain assumptions is given in Appendix B.

2. Predator-prey model assuming group defence. As in Freedman and Wolkowicz [10], we consider 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 prey:

$$\dot{x} = xg(x, K) - yp(x) \triangleq p(x)(F(x, K) - y),$$

$(2.1)_K$
$$\dot{y} = y(-s + q(x)),$$

$$x(0) \geqq 0, \quad y(0) \geqq 0, \quad \cdot = \frac{d}{dt}$$

where $x(t)$ and $y(t)$ denote the density of prey and predator populations, respectively. It is assumed that the functions g, p, and q are continuously differentiable (additional smoothness assumptions are given below) and that s and K are positive constants. When reference is made to model $(2.1)_K$, if there is no ambiguity, the subscript K shall be omitted. Here, $g(x, K)$ represents the specific growth rate of the prey in the absence of predation. Logistic growth, $g(x, K) = r(1 - x/K)$ is considered a prototype.

This leads to the following assumptions on g:
for any $K > 0$

(2.2a) $g(K, K) = 0, \quad g(0, K) > 0, \quad g_K(0, K) \geqq 0, \quad \lim_{K \to \infty} g(0, K)$ is finite,

(2.2b) $g_{xK}(0, K) \geqq 0, \quad g_x(0, K) \leqq 0, \quad \lim_{K \to \infty} g_x(0, K) = 0;$

for any $K > 0$ and $x > 0$

(2.2c) $g_K(x, K) > 0$, $g_{xK}(x, K) > 0$, $g_x(x, K) < 0$, $\lim_{K \to \infty} g_x(x, K) = 0$.

The function $p(x)$ denotes the predator response function and is assumed to satisfy:

(2.3) $p(0) = 0$, $p'(0) > 0$, $p''(0) < 0$, $p(x) > 0$ for $x > 0$.

In order to model group defence, it is assumed as well that there exists $\bar{h} > 0$ such that

(2.4) $p'(x) > 0$ for $0 \leq x < \bar{h}$ and $p'(x) < 0$ for $\bar{h} < x$.

For technical reasons it is assumed that

(2.5) $P(x) \triangleq p(x) - xp'(x) > 0$ for all $x > 0$.

In particular, since $P'(x) = -xp''(x)$ and $P(0) = 0$ it is sufficient to assume that $p(x)$ is concave for $0 < x < \bar{h}$ (since $p'(x) \leq 0$ for $x \geq \bar{h}$, clearly $P(x) > 0$ for $x \geq \bar{h}$).

A function of the form $p(x) = mx/(ax^2 + bx + 1)$ where m, a, and b are positive constants satisfies these assumptions and approximates Holling Type II dynamics (Michaelis–Menten kinetics) for small x.

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. It is assumed that $q(x)$ has properties similar to $p(x)$. In particular

(2.6)
$$q(0) = 0, \quad q(x) > 0 \quad \text{for } x > 0, \quad q(\bar{h}) > s,$$
$$q'(x) > 0 \quad \text{for } 0 \leq x < \bar{h}, \quad \text{and} \quad q'(x) < 0 \quad \text{for } x > \bar{h}.$$

It is also assumed that $q(\bar{h}) > s$ since otherwise the predator cannot survive on the prey at any density. This implies that there exists $\lambda < \bar{h}$ such that $q(\lambda) = s$ and there may exist $\mu > \bar{h}$ such that $q(\mu) = s$.

Other examples of $g(x, K)$, $p(x)$, and $q(x)$ can be found in Boon and Laudelout [3], Holling [12], May [18], Rosenzweig [22], and Yang and Humphrey [27].

The predator isoclines are the vertical lines $x \equiv \lambda$ and $x \equiv \mu$ (provided μ exists). If $\mu > K$ or μ is infinite the asymptotic outcome is the same as in the classical case. It will therefore be assumed that μ is finite throughout the remainder of this paper.

The prey isocline is given by the function $F(x, K) = xg(x, K)/p(x)$. The properties of this function play a key role in the analysis. In particular, we show below that under our assumptions the permissible configurations of the prey isoclines are limited (see Fig. 1). As well, we show that as the carrying capacity K is increased the interior local maximum (if one exists) shifts to the right and the interior local minimum (if one exists) shifts to the left. From this we are able to conclude (see Proposition 2.3) that for K sufficiently large, the prey isocline is monotone for $0 < x < \mu$. This will be used in § 3 to show that there are no periodic orbits or homoclinic orbits possible for sufficiently large K.

Define

(2.7) $F(0, K) = \lim_{x \to 0^+} F(x, K) = g(0, K)/p'(0)$.

Note that $F(0, K) > 0$ and $\lim_{K \to \infty} F(0, K)$ is finite and positive (see (2.2b) and (2.3)). The slope of the prey isocline is given by

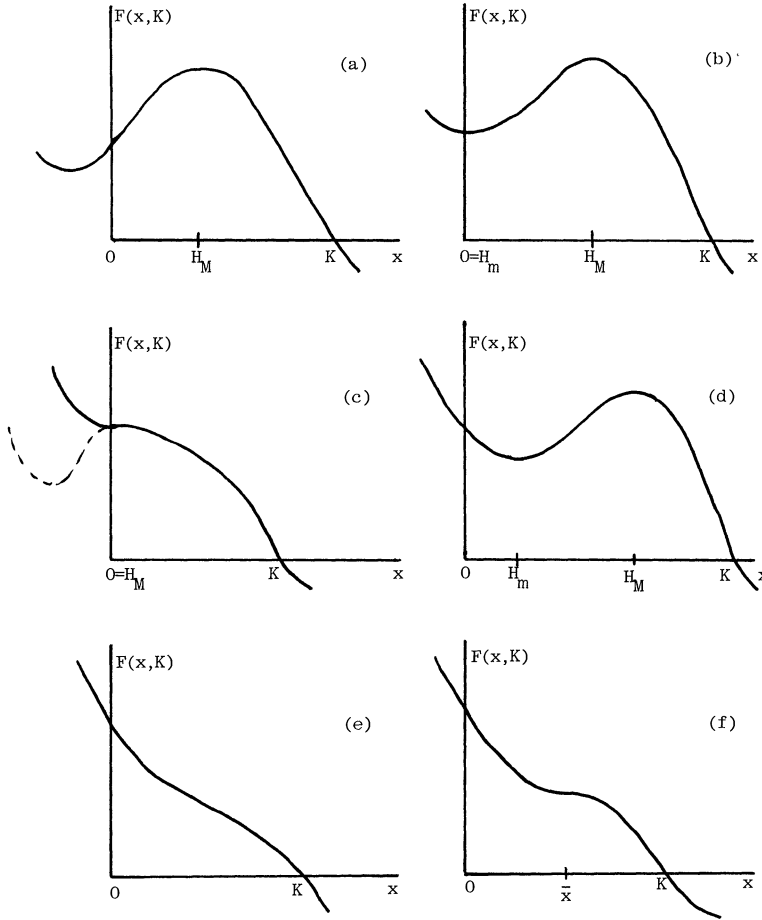(2.8) $F_x(x, K) = (xg_x(x, K)p(x) + g(x, K)(p(x) - xp'(x)))/(p(x))^2$.

FIG. 1. *Permissible configurations of the prey isocline.*

Therefore,

$$(2.9) \qquad\qquad F_x(K, K) = Kg_x(K, K)/p(K) < 0$$

and

$$(2.10) \qquad F_x(0, K) = \lim_{x \to 0^+} F_x(x, K) = (2g_x(0, K)p'(0) - g(0, K)p''(0))/(2(p'(0))^2).$$

Eliminating the possibility of horizontal tangents of $F(x, K)$ and hence of local minima and maxima of the prey isocline over certain parameter ranges will prove useful.

LEMMA 2.1. *Given any* $\gamma > 0$, *there exists* $K^* > \gamma$ *such that for any* $K > K^*$, *if* $0 < \tilde{x} \leqq \gamma$, $F_x(\tilde{x}, K) \neq 0$.

Proof. Suppose the result is false. Then there exist sequences $\{x_n\}$ and $\{K_n\}$ with $0 < x_n \leqq \gamma$ and $\gamma < K_n \to \infty$ as $n \to \infty$ such that $F_x(x_n, K_n) = 0$ for each n. But then by (2.8)

$$(2.11) \qquad\qquad \frac{-g_x(x_n, K_n)}{g(x_n, K_n)} = \frac{p(x_n) - x_n p'(x_n)}{x_n p(x_n)}.$$

However, by (2.2) and the fact that $0 < x_n \leqq \gamma$, it follows that there exist subsequences (relabel for convenience) such that $x_n \to \alpha \geqq 0$, $g(x_n, K_n) \to \beta > 0$ finite, $g_x(x_n, K_n) \to 0$.

But then for these subsequences, $\lim_{n\to\infty}(-g_x(x_n, K_n))/g(x_n, K_n) = 0$. On the other hand,

$$(2.12) \qquad \lim_{n\to\infty}\frac{p(x_n)-x_n p'(x_n)}{x_n p(x_n)} = \begin{cases} \dfrac{p(\alpha)-\alpha p'(\alpha)}{\alpha p(\alpha)} & \text{if } \alpha > 0, \\[2ex] \dfrac{-p''(0)}{2p'(0)} & \text{if } \alpha = 0 \end{cases}$$

which is positive by (2.5) and (2.3), contradicting (2.11). Thus no such subsequences exist and the result follows. □

We continue to investigate how changes in K affect F. Since

$$(2.13) \qquad F_K(x, K) = x g_K(x, K)/p(x) > 0 \quad \text{for } x > 0,$$

F is an increasing function of K for each fixed x. F_{xK} is also an increasing function of K for each fixed $x > 0$ since

$$(2.14) \qquad F_{xK} = (x g_{xK}(x, K)p(x) + g_K(x, K)(p(x) - x p'(x)))/(p(x))^2 > 0$$

by (2.2c) and (2.5).

Remark 2.2. It follows immediately that

(a) if $H_M \triangleq H_M(K)$ is a local maximum of F satisfying $F_x(H_M, K) = 0$, then as K increases, H_M shifts to the right and by Lemma 2.1 is to the right of any fixed $\mu > 0$ for all sufficiently large K, and

(b) if $H_m \triangleq H_m(K)$ is a local minimum of F satisfying $F_x(H_m, K) = 0$, then as K increases, H_m shifts to the left or disappears (i.e., $H_m < 0$) and by Lemma 2.1 disappears for all sufficiently large K.

As a consequence, we have the following proposition.

PROPOSITION 2.3. *Fix $\bar{\mu} > 0$. There exists $K^* > 0$ such that for all $K > K^*$, F has no interior local minimum and any interior local maximum is to the right of $\bar{\mu}$.*

For both biological realism and mathematical convenience, for each $K > 0$, we impose the following restriction on F (see Fig. 1):

$$(2.15) \qquad \text{There are at most two values of } x \in (0, K) \text{ where } F_x(x, K) = 0.$$

This holds for example, if $g(x, K) = r(1 - x/K)$, r a positive constant, and $p(x) = mx/(ax^2 + bx + 1)$ where m, a, and b are positive constants.

Therefore if $F_x(0, K) \geqq 0$, then F has a unique global maximum, say $H_M \geqq 0$ and

$$(2.16) \qquad \begin{aligned} F_x(x, K) &> 0 \quad \text{if } 0 < x < H_M, \\ F_x(x, K) &< 0 \quad \text{if } x > H_M \end{aligned}$$

(see Figs. 1(a)–(c)). In this case we assume $H_m \leqq 0$ or $H_m = -\infty$. If, on the other hand, $F_x(0, K) < 0$, there are three possibilities:

(i) $F_x(x, K) < 0$ for all $x > 0$. Here we assume $H_m \leqq H_M < 0$ or $H_m = -\infty$ (see Fig. 1(e)); or

(ii) there exists a unique point of inflection $\bar{x}$, such that $F_x(x, K) < 0$ for all $x > 0$, $x \neq \bar{x}$ and $F_x(\bar{x}, K) = 0$. Again $H_m \leqq H_M < 0$ or $H_m = -\infty$ (see Fig. 1(f)); or

(iii) there exists a unique positive local minimum H_m and a unique positive local maximum H_M satisfying

$$(2.17) \qquad \begin{aligned} F_x(x, K) &< 0 \quad \text{if } 0 < x < H_m, \\ F_x(x, K) &> 0 \quad \text{if } H_m < x < H_M, \\ F_x(x, K) &< 0 \quad \text{if } H_M < x \end{aligned}$$

(see Fig. 1(d)).

In Appendix B we give an example to show that all the configurations in Fig. 1 are obtainable under our assumptions.

Finally, we observe the following.

Remark 2.4. There can exist at most one pair $(\bar{x}, \bar{K})$ such that $F_x(x, \bar{K}) < 0$ for all $0 < x < \bar{K}$, $x \neq \bar{x}$ and $F_x(\bar{x}, \bar{K}) = 0$ (see Fig. 1(f)). This follows from (2.15), since (2.14) implies that $F_x(\bar{x}, \bar{K} + \varepsilon) > 0$. This forces F to have an interior local maximum, H_M for all $K > \bar{K}$, by Remark 2.2(a). For technical reasons we shall assume that there never exists such a pair $(\bar{x}, \bar{K})$ with $\bar{x} = \lambda$ or μ. This would be an extremely rare coincidence biologically. (This insures that whenever $F_x(\lambda, \hat{K}) = 0$, a Hopf bifurcation occurs as K passes through $\hat{K}$ (see § 4).)

3. Preliminary analytic results. In this section we consider some of the properties of the different invariant sets associated with (2.1).

PROPOSITION 3.1. *The x-axis, y-axis and hence the interior of the first quadrant are all invariant under* $(2.1)_K$. *For each K, solutions for which $x(0) > 0$ and $y(0) > 0$ are (uniformly asymptotically) bounded in positive time and given any $\varepsilon > 0$ these solutions satisfy $x(t) < K + \varepsilon$ for all sufficiently large t.*

Proof. Provided $\lim_{x \to 0} (q(x))/p(x)$ is finite, the proof is similar to the proof given in Hsu [14, Lemma 3.1] (choosing c so that $q(x) - cp(x) \leqq 0$ for all $x \in [0, K+1]$).

If this assumption is omitted, that for each $K > 0$, $y(t)$ is uniformly asymptotically bounded can be shown by fixing any solution for which $x(\tau) = K$ and $y(\tau) > 0$ for some $\tau > 0$, and using a phase plane analysis similar to that given in Freedman [9, pp. 78–80]. Since solutions cannot cross each other, all solutions are eventually trapped inside a region bounded above by this solution. □

There are four possible critical points of $(2.1)_K$. The first two, $M(0) = (0, 0)$ and $M(K) = (K, 0)$ always exist. The other two, $M(\lambda) = (\lambda, F(\lambda, K))$ and $M(\mu) = (\mu, F(\mu, K))$ exist only if $\lambda < K$ and $\mu < K$, respectively, (otherwise $F(\lambda, K) < 0$ and $F(\mu, K) < 0$, respectively). If $\lambda = K$ ($\mu = K$) then $M(\lambda)$ ($M(\mu)$) coalesces with $M(K)$. The stability analysis for these critical points is given in Appendix A and is summarized in Table 1. A typical phase portrait of (2.1) showing how the vector field crosses the isoclines is given in Fig. 2. If $\mu > K$ or $\mu = +\infty$ then the dynamics are basically the same as the dynamics of the classical model in which there is no group defence.

TABLE 1
Linear analysis of critical points.

Critical point	Parameter range			
	$K < \lambda < \mu$	$\lambda < K < \mu$	$\lambda < \mu < K$	
$M(0)$	saddle	saddle	saddle	
$M(K)$	attractor (node)	saddle	attractor (node)	
$M(\lambda)$	*	repellor attractor	repellor attractor	$F_x(\lambda, K) > 0$ $F_x(\lambda, K) < 0$
$M(\mu)$	*	*	saddle	

* This critical point does not exist in this parameter range.

Next consider periodic orbits. The following lemma together with the Poincaré criterion (see Coppel [7]) will be useful to eliminate the possibility of periodic orbits for K in a certain parameter range. It will also be used to show that when periodic orbits do exist they must surround either $(H_m, F(H_m, K))$ or $(H_M, F(H_M, K))$ on the prey isocline.
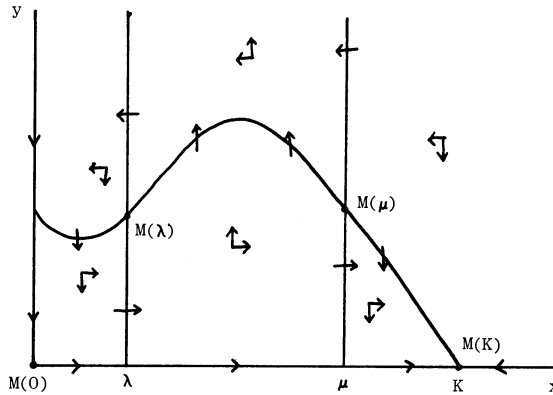
FIG. 2. *Typical vector field of (2.1) for $\mu < K$.*

LEMMA 3.2. *Let Γ be any periodic orbit of (2.1). Then*

$$\Delta \triangleq \oint_\Gamma \text{div } (\dot{x}, \dot{y}) \, dt = \oint_\Gamma p(x) F_x(x, K) \, dt.$$

Proof.

$$\Delta = \oint_\Gamma \text{div } (\dot{x}, \dot{y}) \, dt$$

$$= \oint_\Gamma [(xg_x(x, K) + g(x, K) - yp'(x)) + (-s + q(x))] \, dt$$

$$= \oint_\Gamma \left[\left(xg_x(x, K) + g(x, K) + \left(\frac{\dot{x} - xg(x, K)}{p(x)} \right) p'(x) \right) + \frac{\dot{y}}{y} \right] dt$$

$$= \oint_\Gamma \left[\frac{xg_x(x, K)p(x) + g(x, K)(p(x) - xp'(x))}{p(x)} + \frac{d}{dt} \ln p(x) \right] dt$$

$$= \oint_\Gamma p(x) F_x(x, K) \, dt. \qquad \Box$$

LEMMA 3.3. (a) *There exists $K^* > \mu$ such that for any $K > K^*$, $(2.1)_K$ admits no nontrivial periodic orbits.*

(b) *If K is sufficiently close to λ, $(2.1)_K$ admits no periodic orbits.*

Proof. (a) Observing how the vector field crosses the predator and prey isoclines (see Fig. 2), we note that if a periodic orbit exists it must encircle the critical point $M(\lambda)$. As well, this is the only critical point it can surround.

By Proposition 2.3 we are able to select K^* sufficiently large so that F has no local minima and the global maximum (if it exists) is to the right of μ. Therefore, either

(3.1a)   (i) a local maximum exists and $F_x(x, K) > 0$ for $x \in (0, \mu]$, or

(3.1b)   (ii) no local maximum exists and $F_x(x, K) < 0$ for $x \in (0, \mu]$.

If (i) holds, Lemma 3.2 implies that $\Delta > 0$ and so the Poincaré criterion implies that any periodic orbit is unstable. However, $M(\lambda)$ is also unstable in this parameter range (see Table 1 and Appendix A), a contradiction. In case (ii) the result follows similarly.

(b) The proof is similar to the proof of Proposition 2 in Conway and Smoller [6]. □

Remark 3.4. In an analogous manner one can show that the slope of the portion of the prey isocline inside any periodic orbit cannot be entirely of the same sign. Thus any periodic orbit of $(2.1)_K$ must surround either the point $(H_m, F(H_m, K))$ or $(H_M, F(H_M, K))$.

Next consider homoclinic orbits.

LEMMA 3.5. *There exists $K^* > \mu$ such that for any $K > K^*$, $(2.1)_K$ admits no homoclinic orbits.*

Proof. First we observe that the only critical point that can be involved in a homoclinic orbit is $M(\mu)$ and that any homoclinic orbit must surround $M(\lambda)$. From Lemma 3.3 we can choose K^* such that for all $K > K^*$, $(2.1)_K$ admits no nontrivial periodic orbits and from Proposition 2.3 either (3.1a) or (3.1b) holds. The trace of the variational matrix about $M(\mu)$ (see Appendix A) equals $p(\mu)F_x(\mu, K)$. Thus if a homoclinic orbit exists it must be of the same stability as $M(\lambda)$ (see Chow and Hale [5, Thm. 3.3, p. 357] or Andronov et al. [2, Thm. 44, p. 304]). But this is impossible since there are no periodic orbits surrounding $M(\lambda)$. □

Remark 3.6. Similarly it follows that any homoclinic orbit of (2.1) must enclose either a local minimum of F or a local maximum of F.

An immediate and important consequence of what we have shown is the following theorem.

THEOREM 3.7. *Assume that for some $\tilde{K} > 0$, F has a local maximum at $(H_M, F(H_M, \tilde{K}))$. There exists $K^* > \mu$ such that if $K > K^*$, then all solutions of $(2.1)_K$ with positive initial conditions converge to $M(K)$ except those originating on the stable manifold of $M(\mu)$ or at the point $M(\lambda)$.*

Proof. From Remark 2.2(a) it follows that F has a local maximum for all $K > \tilde{K}$. By Lemmas 3.3 and 3.5, $(2.1)_K$ admits no periodic orbits or homoclinic orbits and all solutions are bounded for positive time by Proposition 3.1. $M(\mu)$ is a saddle and for sufficiently large K, $H_M > \mu$ and $H_m < 0$ and so $F_x(\lambda, K) > 0$ implying that $M(\lambda)$ is a repellor. The result follows (see Fig. 3). □
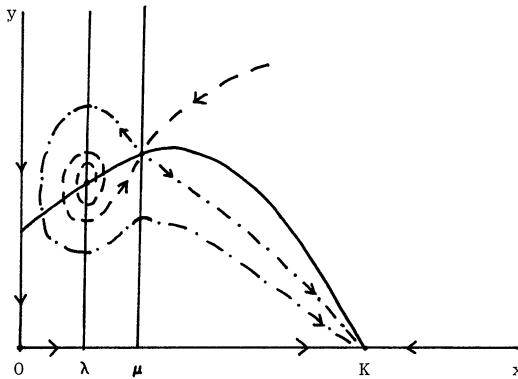
FIG. 3. *Typical phase portrait for sufficiently large K. Almost all solutions converge to M(K). - - - stable manifold of M(μ); - · - · - unstable manifold by M(μ).*

Thus the model predicts that too much enrichment always results in the extinction of the predator unless the prey isocline is monotone decreasing for all values of the carrying capacity K.

PROPOSITION 3.8. *Assume $F_x(x, K) < 0$ for all $K > \mu$ and all $0 < x < K$. Then the stable manifold of $M(\mu)$ separates the positive quadrant into two regions. Solutions*

originating in the inner region all converge to $M(\lambda)$. Solutions with initial conditions in the outer region all converge to $M(K)$ (see Fig. 4).

    Proof. This is an immediate consequence of Remarks 3.4 and 3.6.   □

4. Bifurcation analysis. In this section the dynamics of (2.1) are investigated as K is varied.

    Assumption 4.1. Since the dynamics are more interesting and the model more realistic biologically, it is assumed that the prey isocline has a local maximum for at least one value of $\check{K} > 0$ (and hence for all $K > \check{K}$ by Remark 2.2(a)). (Otherwise $F(x, K)$ is strictly monotonically decreasing for all $K > 0$, $M(\lambda)$ is asymptotically stable, by Remarks 3.4 and 3.6 there are no periodic orbits or homoclinic orbits, and if $\lambda < \mu < K$, the dynamics are the same as those shown in Fig. 4.)

    First note that $M(0)$ undergoes no bifurcations. It remains a saddle for all K with stable manifold along the y-axis and unstable manifold along the x-axis. For $\lambda > K$, $M(K)$ is an asymptotically stable critical point. At $\lambda = K$, $M(\lambda)$ and $M(K)$ coalesce. As K increases, $M(K)$ loses stability becoming a saddle, whereas $M(\lambda)$ enters the first quadrant as an asymptotically stable critical point. We call this bifurcation a λ-exchange. Similarly, for $\mu = K$, $M(\mu)$ and $M(K)$ coalesce. As K increases further, $M(K)$ regains its stability and $M(\mu)$ enters the first quadrant as a saddle and remains a saddle for all K. We refer to this bifurcation as a μ-exchange.

    Since any periodic orbit must surround $M(\lambda)$ and cannot surround any other critical point, $M(\lambda)$ is the only candidate for a Hopf bifurcation. Since our system is planar, and solutions are uniformly asymptotically bounded for each K, though semi-stable periodic orbits may appear and disappear spontaneously, the only way stable or unstable periodic orbits can appear or disappear is either in pairs (one stable and one unstable, see Andronov et al. [2, Chap. 13, pp. 399–401 and p. 432]), or through a homoclinic or Hopf bifurcation. See also Alexander and Yorke [1].

    Under Assumption 4.1 it will be shown that as K increases there is always a Hopf bifurcation about $M(\lambda)$ and a homoclinic bifurcation involving $M(\mu)$.

    First the Hopf bifurcation is examined. The variational matrix about $M(\lambda)$ is (see Appendix A):

(4.1) $$V(M(\lambda)) = \begin{bmatrix} p(\lambda)F_x(\lambda, K) & -p(\lambda) \\ F(\lambda, K)q'(\lambda) & 0 \end{bmatrix}.$$
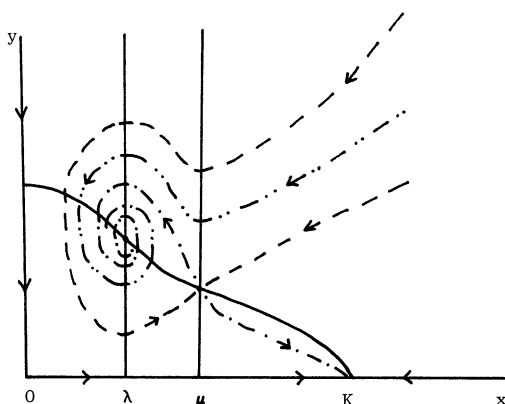

FIG. 4. *Phase portrait of $F_x(x, K) < 0$ for all $x \in (0, K)$ $(K < \mu)$. - - - stable manifold of $M(\mu)$, $E^s_{M(\mu)}$; - · - · - unstable manifold of $M(\mu)$; · · · - · · · stable manifold of $M(\lambda)$. Solutions inside the region defined by $E^s_{M(\mu)}$ converge to $M(\lambda)$. Outside the region defined by $E^s_{M(\mu)}$ solutions converge to $M(K)$.*

Therefore the characteristic equation is:

(4.2) $$\gamma^2 - \gamma p(\lambda) F_x(\lambda, K) + F(\lambda, K) q'(\lambda) = 0,$$

with roots:

$$\gamma(K) = \frac{p(\lambda) F_x(\lambda, K) \pm \sqrt{(p(\lambda) F_x(\lambda, K))^2 - 4F(\lambda, K) q'(\lambda)}}{2}.$$

The roots are therefore purely imaginary if and only if $F_x(\lambda, \hat{K}) = 0$ and are complex in a neighbourhood of $\hat{K}$. Since $\text{Re}\,(\gamma(\hat{K})) = 0$, $\text{Im}\,(\gamma(\hat{K})) \neq 0$ and

$$\frac{d}{dK}\,\text{Re}\,\gamma(\hat{K}) = p(\lambda)\,\frac{F_{xK}(\lambda, \hat{K})}{2} > 0$$

by (2.14), there is a Hopf bifurcation at $K = \hat{K}$. That there exists a unique $\hat{K}$ such that $F_x(\lambda, \hat{K}) = 0$ follows from Remarks 2.4 and 2.2. Therefore there is only one value of K for which there is a Hopf bifurcation. From Remark 2.2 it follows as well that $(\lambda, \hat{K})$ is either a local minimum or a local maximum of the prey isocline. The direction and stability of the bifurcating periodic orbit is determined by the sign of the quantity:

(4.3) $$w = \frac{-p(\lambda) F_{xx}(\lambda, \hat{K}) q''(\lambda)}{q'(\lambda)} + p(\lambda) F_{xxx}(\lambda, \hat{K}) + 2p'(\lambda) F_{xx}(\lambda, \hat{K}),$$

which was determined using the algorithm in Marsden and McKracken [17] and the symbol manipulation package REDUCE. This generalizes the condition given in Conway and Smoller [6]. We summarize the details in the following proposition.

PROPOSITION 4.2. *If $w < 0$ the bifurcating periodic orbit is orbitally stable and exists provided $K > \hat{K}$ and $|K - \hat{K}|$ sufficiently small. If $w > 0$ then the bifurcating periodic orbit is unstable and exists provided $K < \hat{K}$ and $|K - \hat{K}|$ sufficiently small.*

Remark 4.3. If $w > 0$ and $(\lambda, \hat{K})$ is a local maximum of the prey isocline it follows (from Lemma 3.3(b)) that for some $K < \hat{K}$ there is either the spontaneous appearance of (a semistable periodic orbit which splits into) a pair of stable and unstable periodic orbits or a Hopf bifurcation and a homoclinic bifurcation occur simultaneously (because the outermost periodic orbit must be asymptotically stable). If the Hopf bifurcation occurs before the μ-exchange, then only the former scenario is possible.

Next, the homoclinic bifurcation is investigated. This will be done by means of a phase plane argument, focusing attention on the stable and unstable manifolds, $E^s_{M(\mu)}$ and $E^u_{M(\mu)}$, of $M(\mu)$. Consider that part of $E^s_{M(\mu)}(E^u_{M(\mu)})$ that approaches (leaves) $M(\mu)$ from (towards) the left and call it $\Gamma^s(\Gamma^u)$. Freedman and Wolkowicz [10] point out that there are at most three possibilities for Γ^s (see Fig. 5).

Case 1. In negative time Γ^s leaves the strip $0 \leq x \leq \mu$ (Fig. 5(a)). Γ^u must therefore approach (in forward time) $M(\lambda)$ or a periodic orbit enclosing $M(\lambda)$.

Case 2. Γ^s is a homoclinic orbit, that is $\Gamma^s = \Gamma^u$ (Fig. 5(b)).

Case 3. Γ^s remains in the strip $0 \leq x < \mu$ for all time and if followed as time is reversed either approaches the outermost periodic orbit surrounding $M(\lambda)$ or $M(\lambda)$ if there are no periodic orbits. In this case Γ^u approaches $M(K)$ (Fig. 5(c)).

In [10], it is shown numerically that for a specific example as K varies, the model exhibits the dynamics in each of the three cases described above. It will be shown analytically that this is true in general (under our assumptions).

Remark 4.4. By Theorem 3.7 (see Fig. 3) it follows that Case 3 holds for all sufficiently large K. If it can be shown that there always exists some $K > 0$ such that Case 1 holds, by continuity it follows that Case 2 must hold for some K as well, and hence there always exists a homoclinic bifurcation. That this is indeed the case is shown below. To do this we consider all the possible sequences of bifurcations.
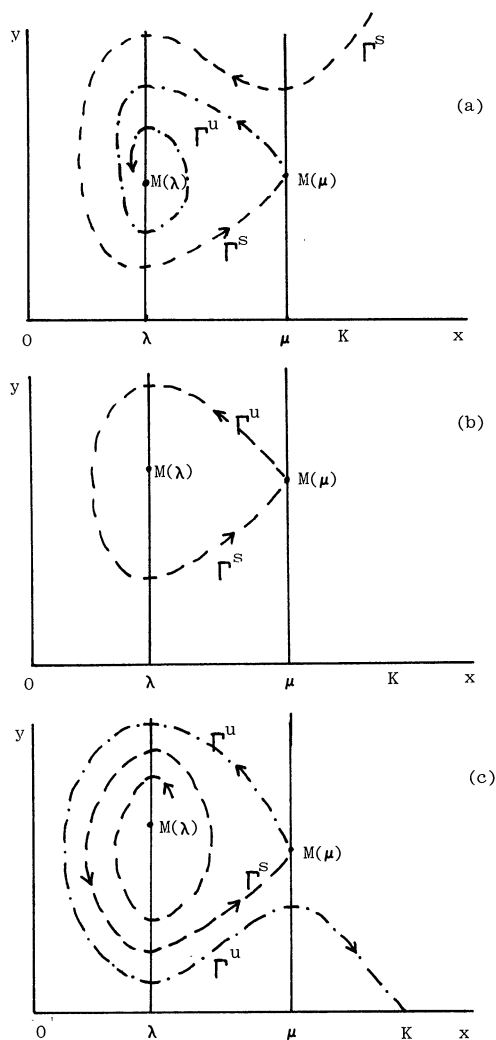
FIG. 5. *Three possibilities for the portion of the stable and unstable manifold of* $M(\mu)$ *to the left of* μ.

Remark 4.5. The bifurcations of model (2.1) as K is increased from $0 < K < \lambda$ will be traced. Though the possibility of the spontaneous appearance and disappearance of periodic orbits surrounding $M(\lambda)$ will be taken into account and the stability properties of the outermost such periodic orbit taken into consideration, in the analysis that follows their occurrence will not be recorded.

If $0 < K < \lambda$, then the first bifurcation to occur as K is increased is a λ-exchange. After a λ-exchange there can only be either a μ-exchange or a Hopf bifurcation.

If the μ-exchange is first, then before the next bifurcation (Hopf or homoclinic) takes place, $M(\lambda)$ remains asymptotically stable, and if any periodic orbits surround $M(\lambda)$, the outermost one must be stable from the outside. This follows since solutions are uniformly asymptotically bounded by Proposition 3.1, and so there can be no bifurcation of periodic orbits from infinity. Though semistable periodic orbits may appear and disappear spontaneously, the only way stable or unstable periodic orbits can appear or disappear is in pairs, one stable and one unstable (see Andronov et al.

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[2, Chap. 13, especially pp. 399–401, 432]) since we have eliminated the possibility of a Hopf or a homoclinic bifurcation. Therefore the dynamics are described by Case 1.

If, on the other hand, the Hopf bifurcation occurs (at $K = \hat{K}$) before the μ-exchange then for $K > \hat{K}$ but close to $\hat{K}$, $M(\lambda)$ is a repellor. The outermost periodic orbit must still be asymptotically stable (whether the Hopf bifurcation was subcritical or supercritical and whether it occurred for $(\lambda, \hat{K})$ a local minimum or a local maximum of the prey isocline). The μ-exchange is the only bifurcation that can follow. Again the dynamics are described by Case 1.

Therefore by Remark 4.4, there is always at least one value of K for which there is a homoclinic orbit and hence a homoclinic bifurcation. Recall that the stability of the homoclinic orbit depends on the trace of the variational matrix at $M(\mu)$, tr $V(M(\mu))$ (see Chow and Hale [5, Thm. 3.3, p. 357] or Andronov et al. [2, Thm. 44, p. 304]). Since tr $V(M(\mu)) = p(\mu)F_x(\mu, K)$, the homoclinic orbit is stable if the prey isocline is strictly decreasing at (μ, K) and unstable if it is strictly increasing. This, together with information concerning the stability of the outermost periodic orbit surrounding $M(\lambda)$, restricts the possible positions of the predator isoclines relative to H_m and H_M at which a homoclinic orbit can occur and hence the possible values of K. Whether or not the homoclinic bifurcation is unique has not been investigated. It is conceivable that the spontaneous appearance and disappearance of pairs of periodic orbits could result in a sequence of homoclinic bifurcations.

In the numerical example given in Freedman and Wolkowicz [10], $\bar{x} < 0$ (see Remark 2.4), and there is a λ-exchange followed by a supercritical Hopf bifurcation $(w < 0)$, at $x = H_M$, a μ-exchange and finally a stable homoclinic bifurcation. Different scenarios are clearly possible, for example a λ-exchange followed by μ-exchange, and then either the homoclinic bifurcation followed by the Hopf bifurcation or the Hopf bifurcation followed by the homoclinic bifurcation. Also the Hopf bifurcation may be subcritical or supercritical and may occur either for $x = H_M$ or $x = H_m$. The homoclinic bifurcation may lead to a stable or an unstable periodic orbit.

5. Discussion. A class of ODEs modeling predator-prey interaction in which the prey are allowed to exhibit group defence was analyzed. It was shown that if the carrying capacity is made sufficiently large by enrichment of the environment, the model predicts the eventual extinction of the predator. This gives strong support to Rosenzweig's warning [22] and suggests that one must proceed with caution when trying to tamper with nature since unexpected outcomes could result.

The weakening of the monotonicity assumption on the predator response function in order to model group defence leads to a model with rich dynamics. Taking the carrying capacity K as the bifurcation parameter, there are several different types of bifurcations including a homoclinic bifurcation.

There are also implications of the results for the classical model (i.e., no group defence allowed). In particular, it is shown that the Hopf bifurcation can be either subcritical or supercritical (see condition (4.3)). It is then easy to construct a predator-prey model in which there is a semi-stable periodic orbit for some value of K that splits into a pair (one stable and one unstable) of periodic orbits as K varies (see Remark 4.3). The question of the number of periodic orbits for predator-prey systems and in particular of uniqueness of the periodic orbit is intriguing and apparently difficult. Cheng [4] (with minor modifications required) proves uniqueness for a special case of $(2.1)_K$. He assumes that p and q are modeled by Holling Type II dynamics, and g by logistic growth. Thus F, the prey isocline is symmetric about its maximum, H_M. Conway and Smoller [6] extend his proof to other systems for which the prey

isocline is symmetric about H_M. However, it seems that the structure of the models in both [4] and [6] play a role since symmetry alone does not imply uniqueness. This can be seen since symmetry implies $F_{xxx}(H_M, K) = 0$ and so (4.3) reduces to

$$w = F_{xx}(\lambda, \hat{K})\left(-p(\lambda)\frac{q''(\lambda)}{q'(\lambda)} + 2p'(\lambda)\right).$$

Since $F_{xx}(\lambda, \hat{K}) < 0$ at $\lambda = H_M$ it follows that the sign of w depends on p and q and their derivatives. In particular if $q''(\lambda)/q'(\lambda) > 2p'(\lambda)/p(\lambda)$, $w > 0$, and by Remark 4.3 there are at least two periodic orbits. Since q plays no role in determining F, it is no problem to find an appropriate q, which of course would have to be convex at λ (e.g., sigmoidal dynamics would work). Perhaps symmetry and concavity of q at λ imply uniqueness. Of course, symmetry is not necessary for uniqueness.

Appendix A. Linear analysis of (2.1)$_K$. Let $E^* = (x^*, y^*)$ denote any equilibrium of (2.1). In the case $\mu = +\infty$, the stability analysis is given in Freedman [8], [9]. For μ finite the analysis is described in Freedman and Wolkowicz [10].

For completeness we summarize the stability analysis of the critical points.
The variational matrix about any equilibrium (x^*, y^*) is:

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

$M(0)$ is always a saddle. $M(K)$ is a saddle if $\lambda < K < \mu$ and is a stable node if $\lambda > K$ or $\mu < K$.

If both $x^* \neq 0$ and $y^* \neq 0$, then

$$V(x^*, y^*) = \begin{bmatrix} p(x^*)F_x(x^*, K) & -p(x^*) \\ y^*q'(x^*) & 0 \end{bmatrix}.$$

Therefore the characteristic equation is:

$$\gamma^2 - \gamma p(x^*)F_x(x^*, K) + y^*p(x^*)q'(x^*) = 0.$$

If $K < \lambda < \mu$, $M(0)$ and $M(K)$ are the only critical points and $M(K)$ is a global attractor with respect to the interior of the first quadrant.

If $\lambda < K < \mu$ then the stability of $M(\lambda)$ depends on the slope of $F_x(\lambda, K)$. If $F_x(\lambda, K) < 0$ then $M(\lambda)$ is asymptotically stable. If $F_X(\lambda, K) > 0$ then $M(\lambda)$ is unstable. $V(M(\lambda))$ has nontrivial, pure imaginary eigenvalues if, and only if, $F_x(\lambda, K) = 0$. If for λ fixed and some $\hat{K}$, $F_x(\lambda, \hat{K}) = 0$, then selecting K as the bifurcation parameter, it can be shown that at $\hat{K}$ there is a Hopf bifurcation (either subcritical or supercritical).

If $\lambda < \mu < K$, then $M(\mu)$ is a saddle. The stability of $M(\lambda)$ depends on the sign of $F_x(\lambda, K)$ just as in the previous case and the criteria for the Hopf bifurcation are also the same as before.

Note that unless $\lambda = K$, $\mu = K$ or $F_x(\lambda, K) = 0$ all critical points are hyperbolic.

Appendix B. Example. We include the following example to show that all the configurations in Fig. 1 are obtainable under our assumptions.

Let $p(x) = mx/(ax^2 + bx + 1)$ where m, a, b are positive constants, and $g(x, K) = r(1 - x/K)$ where r is a positive constant. Then

$$F(x, K) = \frac{r}{mK}(K - x)(ax^2 + bx + 1),$$

$$F_x(x, K) = \frac{r}{mK}[(Kb - 1) + x(2aK - 2b) - 3ax^2],$$

and so

$$F_x(0, K) > 0 \quad \text{if } Kb > 1,$$
$$= 0 \quad \text{if } Kb = 1,$$
$$< 0 \quad \text{if } Kb < 1.$$

Also

$$F_{xx}(x, K) = (r/mK)[2aK - 2b - 6ax].$$

To obtain Fig. 1(a) take $Kb > 1$. To obtain Fig. 1(b) take $Kb = 1$ and $aK > b$. To obtain Fig. 1(c) take $Kb = 1$ and $aK - b \leqq 0$. To obtain Fig. 1(d) one requires only that $aK > b$, $Kb < 1$, and $bK + aK^2 + b^2/a > 3$. This is clearly possible since one can choose K and b so that $Kb < 1$ and then we can take a as large as we need. For Fig. 1(e) let $Kb < 1$ and $bK + aK^2 + b^2/a < 3$ and for Fig. 1(f) let $Kb < 1$, $aK > b$ and $bK + aK^2 + b^2/a = 3$.

REFERENCES

[1] J. C. ALEXANDER AND J. A. YORKE, Global bifurcations of periodic orbits, Amer. J. Math., 100 (1978), pp. 263–292.

[2] A. A. ANDRONOV, E. A. LEONTOVICH, I. I. GORDON, AND A. G. MAIER, Theory of Bifurcations of Dynamical Systems on a Plane, John Wiley, New York, 1973.

[3] B. BOON AND H. LAUDELOUT, Kinetics of nitrite oxydation by Nitrobacter Winogradski, Biochem. J., 85 (1962), pp. 440–447.

[4] K. S. CHENG, Uniqueness of a limit cycle for a predator-prey system, SIAM J. Math. Anal., 12 (1981), pp. 541–548.

[5] S. N. CHOW AND J. K. HALE, Methods of Bifurcation, Springer-Verlag, New York, 1982.

[6] E. D. CONWAY AND J. A. SMOLLER, Global analysis of a system of predator-prey equations, SIAM J. Appl. Math. 46 (1986), pp. 630–642.

[7] W. A. COPPEL, Stability and Asymptotic Behaviour of Differential Equations, D. C. Heath, New York, 1965.

[8] H. I. FREEDMAN, Graphical stability, enrichment, and pest control by a natural enemy, Math. Biosci., 31 (1976), pp. 207–225.

[9] ———, Deterministic Mathematical Models in Population Ecology, Marcel Dekker, New York, 1980.

[10] H. I. FREEDMAN AND G. S. K. WOLKOWICZ, Predator-prey systems with group defense: the paradox of enrichment revisited, Bull. Math. Biol., 48 (1986), pp. 493–508.

[11] M. E. GILPIN, Enriched predator-prey systems: theoretical stability, Science, 177 (1972), pp. 902–904.

[12] C. S. HOLLING, The functional response of predators to prey density and its role in mimicry and population regulation, Mem. Entomolog. Soc. Canada, 45 (1965), pp. 3–60.

[13] J. C. HOLMES AND W. M. BETHEL, Modification of intermediate host behaviour by parasites, Zoolog. J. Linnean Soc., Suppl. 1, 51 (1972), pp. 123–149.

[14] S. B. HSU, On global stability of a predator-prey system, Math. Biosci., 39 (1978), pp. 1–10.

[15] C. B. HUFFAKER, K. P. SHEA, AND S. G. HERMAN, Experimental studies on predation: Complex dispersion and levels of food in an alarine predator-prey interaction, Hilgardia, 34 (1963), pp. 305–329.

[16] L. S. LUCKINBILL, Coexistence in laboratory populations of Paramecium Aurelia and its predator Didinium Nastum, Ecology, 54 (1973), pp. 1320–1327.

[17] J. E. MARSDEN AND M. MCKRACKEN, The Hopf Bifurcation and its Applications, Springer-Verlag, New York, 1976.

[18] R. M. MAY, Limit cycles in predator-prey communities, Science, 177 (1972), pp. 900–902.

[19] C. D. MCALLISTER, R. J. LEBRASSEUR, AND T. R. PARSONS, Stability of enriched aquatic ecosystems, Science, 175 (1972), pp. 564–565.

[20] K. MISCHAIKOW AND G. S. K. WOLKOWICZ, A predator-prey model involving group defence: A connection matrix approach, in Mathematical Ecology: Proceedings of the Research Conference, Trieste (1986), L. J. Gross, T. G. Hallam and S. A. Levin, eds., World Scientific Publishing Co.

[21] J. F. RIEBESELL, Paradox of enrichment in competitive systems, Ecology, 55 (1974), pp. 183–187.

[22] M. L. ROSENZWEIG, Paradox of enrichment: destabilization of exploitation ecosystems in ecological time, Science, 171 (1971), pp. 385–387.

[23] ———, Reply to McAllister et al., Science, 175 (1972), pp. 564–565.

[24] ———, *Reply to Gilpin*, Science, 177 (1972), p. 904.
[25] W. M. SCHAFFER AND M. L. ROSENZWEIG, *Homage to the red queen* I. *Coevolution of predators and their victims*, Theoret. Population Biol., 14 (1978), pp. 135–157.
[26] J. S. TENER, *Muskoxen*, Queen's Printer, Ottawa, 1965.
[27] R. D. YANG AND A. E. HUMPHREY, *Dynamics and steady state studies of phenol biodegradation in pure and mixed cultures*, Biotechnol. Bioeng., 17 (1975), pp. 1211–1235.