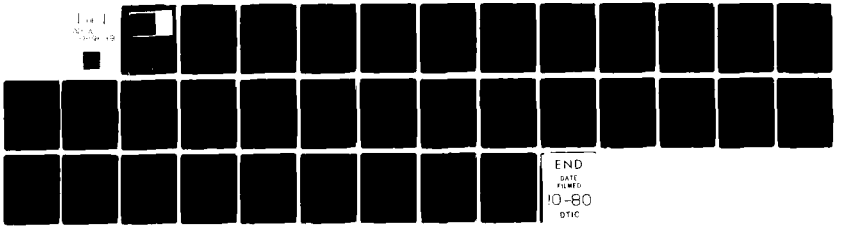
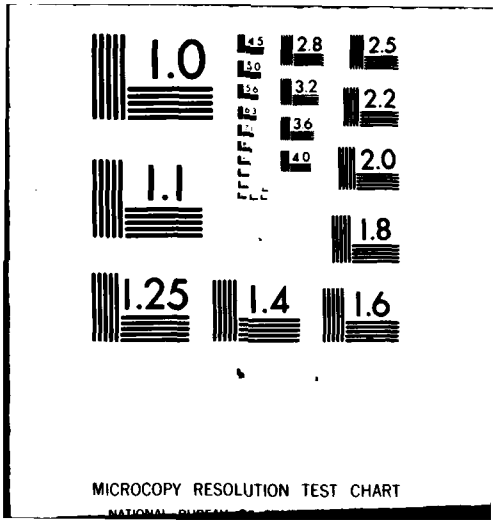
AD-A089 639 WISCONSIN UNIV-MADISON MATHEMATICS RESEARCH CENTER F/G 12/2
COEXISTENCE PROPERTIES OF SOME PREDATOR-PREY SYSTEMS UNDER CONS--ETC(U)
AUG 80 F BRAUER, A C SOUDACK DAAG29-80-C-0041
UNCLASSIFIED MRC-TSR-2101 NL



END
DATE FILMED
10-80
DTIC


1.0
1.1
1.25
1.4
1.6
1.8
2.0
2.2
2.5
2.8
3.2
3.6
4.0
MICROCOPY RESOLUTION TEST CHART

LEVEL II

AD A089639

(9) MRC Technical Summary Report #2101

(6) COEXISTENCE PROPERTIES OF SOME PREDATOR-PREY SYSTEMS UNDER CONSTANT RATE HARVESTING AND STOCKING.

(10) F. Brauer and A. C. Soudack

Mathematics Research Center
University of Wisconsin—Madison
610 Walnut Street
Madison, Wisconsin 53706

(14) MRC-TR-2101

(11) August 1980

(Received May 29, 1980)

DTIC ELECTE SEP 29 1980 A

Approved for public release
Distribution unlimited

FILE COPY

Sponsored by

U. S. Army Research Office
P. O. Box 12211
Research Triangle Park
North Carolina 27709

80 9 24 046

COEXISTENCE PROPERTIES OF SOME PREDATOR-PREY SYSTEMS UNDER CONSTANT RATE HARVESTING AND STOCKING*

by

F. Brauer[1] and A. C. Soudack[2]

Technical Summary Report #2101

August 1980

ABSTRACT

The global behaviour of a class of predator-prey systems, modelled by a pair of non-linear ordinary differential equations, under constant rate harvesting and/or stocking of both species, is presented. Theoretically possible structures and transitions are developed and validated by computer simulations. The results are presented as transition loci in the F-G (prey harvest rate - predator harvest rate) plane.

AMS (MOS) Subject Classifications: 34A34, 34D30, 58F21, 92A15, 92A17

Key Words: Predator-prey systems, Harvesting, Stability.

Work Unit Number 1 - Applied Analysis

---

[1]Department of Mathematics, University of Wisconsin-Madison, Madison, Wisconsin 53706.

[2]Department of Electrical Engineering, University of British Columbia, Vancouver, B. C., V6T 1W5, Canada.

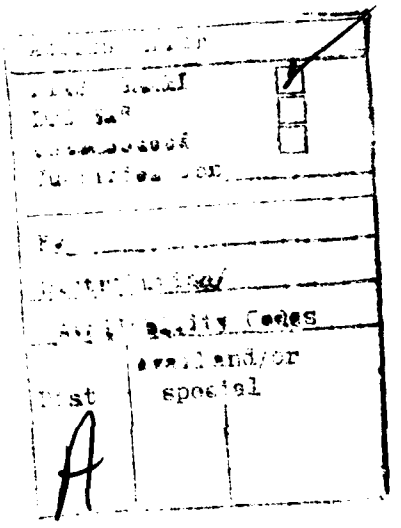
---

*Sponsored by the United States Army under Contract No. DAAG29-80-C-0041 and in part by NSERC of Canada, Grant No. 67-3138.

SIGNIFICANCE AND EXPLANATION

This report gives general and complete results on the coexistence of predator-prey systems under constant rate harvesting and stocking. A theoretical analysis is presented and a number of computer simulations are included. Certain phenomena not included in the analysis are uncovered.

The significance of the work is in showing that different structures of the system can exist, that coexistence regions decrease as harvest rates increase, and that contrary to indications given by system linearization, collapse can occur well before mathematically critical harvest rates are reached. This information should be useful in resource management programs.



COEXISTENCE PROPERTIES OF SOME PREDATOR-PREY SYSTEMS UNDER CONSTANT RATE HARVESTING AND STOCKING*

by

F. Brauer[1] and A. C. Soudack[2]

1. Introduction

In a sequence of papers [Brauer, Soudack and Jarosch (1976); Brauer and Soudack (1979a); Brauer and Soudack (1979b); Brauer and Soudack (1980)], we have analyzed the global behaviour of predator-prey systems under constant rate harvesting of either species and under constant rate stocking (which may be viewed as negative harvesting) of either species and of both species simulataneously. In all of this previous work, the focus of our attention has been on the nature of the phase portrait for a given harvest rate and on the transitions between types of behaviours as the harvest rate is changed.

In this paper we generalize our earlier results to allow two independent constant harvest rates (positive or negative) for the two species. We also make a slight change in emphasis and concentrate on classification of regions in the harvest-rate plane rather than on the phase portraits. Of course, the phase portrait analysis can also be carried out, and some such analysis is necessary for the desired classification of regions. However, we have chosen to suppress much of this detail in order to concentrate on the question of

[1]Department of Mathematics, University of Wisconsin-Madison, Madison, Wisconsin 53706.

[2]Department of Electrical Engineering, University of British Columbia, Vancouver, B.C., V6T 1W5, Canada.

*Sponsored by the United States Army under Contract No. DAAG29-80-C-0041 and in part by NSERC of Canada, Grant No. 67-3138.

what qualitative behaviour is to be expected under changes of one or both harvest rates. Even though the class of models studied is unrealistically simple, our results imply warnings about unexpected dangers which may be relevant to the management of real-life systems.

2. General Theory

We consider the system

$$\begin{aligned} x' &= x\, f(x,y) - F \\ y' &= y\, g(x,y) - G \end{aligned} \tag{1}$$

as a model for the sizes $x(t)$ of a prey population and $y(t)$ of a predator population. Here, $f(x,y)$ and $g(x,y)$ are the respective per capita growth rates of the two population sizes. As in our previous work [Brauer, Soudack and Jarosch (1976); Brauer and Soudack (1979a); Brauer and Soudack (1979b); Brauer and Soudack (1980)] we assume that these depend only on the population sizes at time t. The prey species is harvested at a constant time rate F, while the predator species is harvested at a constant time rate G. We permit either F, or G, or both, to be negative, to represent stocking rather than harvesting of the corresponding species.

The predator-prey nature of the model is expressed by the assumptions

$$f_x(x,y) < 0, \quad g_x(x,y) > 0, \quad g_y(x,y) \leq 0 \tag{2}$$

for $x > 0$, $y > 0$ (subscripts denoting partial derivatives. These assumptions imply that the equation $g(x,y) = 0$, representing the (unharvested) predator isocline, defines x as a monotone non-decreasing function $x = \Gamma(y)$ for $0 < y < \infty$. We assume that this isocline intersects the x-axis at $(J,0)$; that is, that $J = \Gamma(0)$, or

$$g(J,0) = 0 \quad . \tag{3}$$

As we have pointed out previously (Brauer and Soudack (1979a)), in many of the commonly-used models for function g is independent of y, corresponding to the situation in which the predators do not interfere with one another in their search for prey. In this case the predator isocline $g(x,y) = 0$ is the vertical line $x = J$.

The hypothesis (2) also implies that the equation $f(x,y) = 0$, representing the (unharvested) prey isocline, defines y as a single-valued function $y = \Phi(x)$ which we assume non-negative on an interval $0 \leq \alpha \leq x \leq K \leq \infty$ with $\Phi(K) = 0$, or

$$f(K,0) = 0 \quad . \tag{4}$$

It is necessary to distinguish three possibilities, as follows:

(i) $\alpha > 0$, corresponding to $f(0,0) < 0$.

(ii) $\alpha = 0$, corresponding to $f(0,0) > 0$, and there exists $L < \infty$ such that

$$f(0,L) = 0 \tag{5}$$

(iii) $\alpha = 0$, $L = \infty$.

Biologically, $\alpha > 0$ is the case in which the prey population is unable to develop if it gets too small, even in the absence of predators. If $\alpha = 0$, the prey population can establish itself from a small initial population; L is the maximum predator density for which the prey population can establish itself. If $\alpha = 0$, $L = \infty$, the prey population can establish itself for any predator population. Finally, we assume

$$\alpha < J < K \ . \tag{6}$$

The cases $J > K$ and $J < \alpha$ may be analyzed by the same methods and are essentially trivial. A discussion of the biological significance of the numbers α, J, K, L may be found in [Brauer and Soudack (1979a)].

An equilibrium $\hat{P}(\hat{x},\hat{y})$ of the system (1) is an intersection of the prey isocline $xf(x,y) - F = 0$ and the predator isocline $yg(x,y) - G = 0$. To study the (local) stability of an equilibrium, we linearize about the equilibrium, forming the matrix

$$\Delta(P) = \begin{matrix} \hat{x}\, f_x(\hat{x},\hat{y}) + f(\hat{x},\hat{y}) & \hat{x}\, f_y(\hat{x},\hat{y}) \\ \hat{y}\, g_x(\hat{x},\hat{y}) & \hat{y}\, g_y(\hat{x},\hat{y}) + g(\hat{x},\hat{y}) \end{matrix}$$

and then determine the eigenvalues of $\Delta(\hat{P})$. In particular, if $\det \Delta(\hat{P}) < 0$, then the eigenvalues have opposite sign and $\hat{P}$ is a saddle point. If $\det \Delta(\hat{P}) > 0$, then the real parts of the eigenvalues have the same sign and $\hat{P}$ is a node or spiral point which is asymptotically stable if $\operatorname{tr} \Delta(\hat{P}) < 0$ and unstable if $\operatorname{tr} \Delta(\hat{P}) > 0$ (corresponding to eigenvalues with negative real part and positive real part respectively).

If $G \neq 0$, the predator isocline $y\, g(x,y) = G$ is a curve which approaches the curve $g(x,y) = 0$ asymptotically. The portion of this curve in the first quadrant lies to the right of $g(x,y) = 0$ if $G > 0$ and to the left of $g(x,y) = 0$ if $G < 0$.

To describe the prey isocline $x\, f(x,y) = F$ for $F \neq 0$, we define

$$f^*(x,y) = f(x,y) - \frac{F}{x} \quad .$$

Then the prey isocline is the curve $f^*(x,y) = 0$; we shall regard $f^*(x,y)$ as a modified per capita growth rate for each fixed F. It is easy to see that for every $F < 0$, f^* satisfies the same hypotheses as f and is of the type $\alpha = 0$, $L = \infty$, independent of the type for $F = 0$. For $F > 0$, there are two critical values of F. For sufficiently small $F > 0$, f^* satisfies the same hypotheses as f and is of the type $\alpha > 0$, with $\alpha = \alpha(F) < J$ and $K = K(F) > J$. There exists $F_c > 0$ such that either

(i) $\alpha(F_c) < J$, $K(F_c) = J$

or

(ii) $\alpha(F_c) = J$, $K(F_c) > J$.

Further, there exists $F^* > F_c$ for which

$$\alpha(F^*) = K(F^*)$$

[Brauer and Soudack (1979b)]. Then f^* satisfies the same hypotheses as f and is of the type $\alpha > 0$ for $0 < F < F^*$.

This suggests that models of the type $\alpha > 0$ with $F = 0$ may be the result of some harvesting of prey by biological mechanisms outside the system, while models of the type $\alpha = 0$, $L = \infty$ may represent some external stocking of prey. Models with $\alpha = 0$, $L < \infty$ which are the type most frequently studied, represent a critical balance between external harvesting and stocking.

For each suitably chosen fixed F, we may now view the system (1) as a pure predator harvesting or stocking model

$$\begin{aligned} x' &= x\, f^*(x,y) \\ y' &= y\, g(x,y) - G \quad , \end{aligned} \tag{7}$$

with the prey harvest or stocking built into the prey growth rate. Thus as G is varied for any fixed F, the possible transitions are of the same types as for pure predator

harvesting (Brauer and Soudack (1979a)). The first question we wish to examine is the existence of an equilibrium of the system (1), or (7), in the interior of the first quadrant. It is known [Brauer and Soudack (1979a)] that there exists $G^+ = G^+(F) > 0$ such that the system (1) has an equilibrium $P_\infty = P_\infty(F,G)$, not a saddle point, in the interior of the first quadrant of the x-y plane if $0 \leq G < G^+$, and has no equilibrium in the interior of the first quandrant if $G > G^+$. This holds for all $F < 0$ and for sufficiently small positive F. It is easy to see graphically that $G^+(F)$ must be a monotone decreasing function of F for $-\infty < F < \infty$.

If $G < 0$ we must distinquish between the cases $F > 0$ and $F < 0$ because of the difference between the cases $\alpha > 0$ and $\alpha = 0$, $L = \infty$, [Brauer and Soudack (1980)]. If $F > 0$, corresponding to $\alpha > 0$, there exists $G^- = G^-(F) < 0$ such that the system (1) has an equilibrium $P_\infty = P_\infty(F,G)$ (not a saddle point) in the interior of the first quadrant if $0 > G > G^-$, and has no equilibrium in the interior of the first quadrant if $G < G^-$. It is easy to see that $G^-(F)$ is a monotone incresing function of F. If $F < 0$, corresponding to $\alpha = 0$, $L = \infty$, the system (1) has an equilibrium P_∞ in the interior of the first quadrant for all $G < 0$.

The above analysis is valid for all $F < 0$, but for positive F it is obviously valid only for $0 \leq F < F_c$. However, if $\alpha(F_c) < J$, $K(F_c) = J$ and $G < 0$, it is easy to see that it is in fact valid for $0 \leq F < F^*$. Similarly, if $\alpha(F_c) = J$, $K(F_c) > J$, and $G > 0$, it is valid for $0 \leq F < F^*$. We may collect this information on the values of the harvest rates F and G for which there is an equilibrium $P_\infty = P_\infty(F,G)$ in the interior of the first quadrant of the x-y plane. In Figures 1 and 2, the interior of the shaded region indicates the set R of such values in the F-G plane. Such figures have been given before for species in competition [Yodzis (1976), Reading (unpublished), Griffel (1979)].

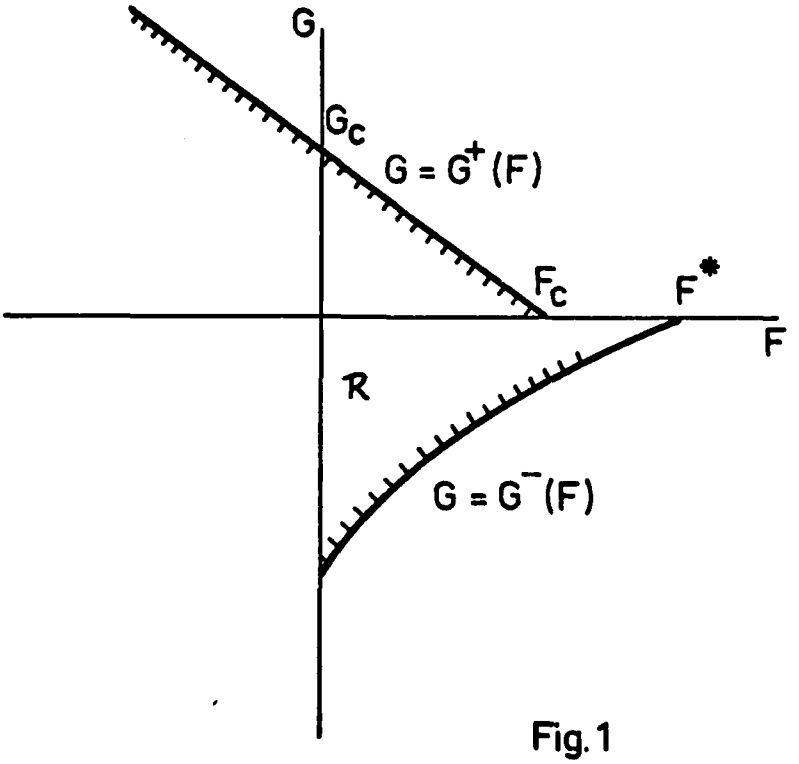


Fig. 1

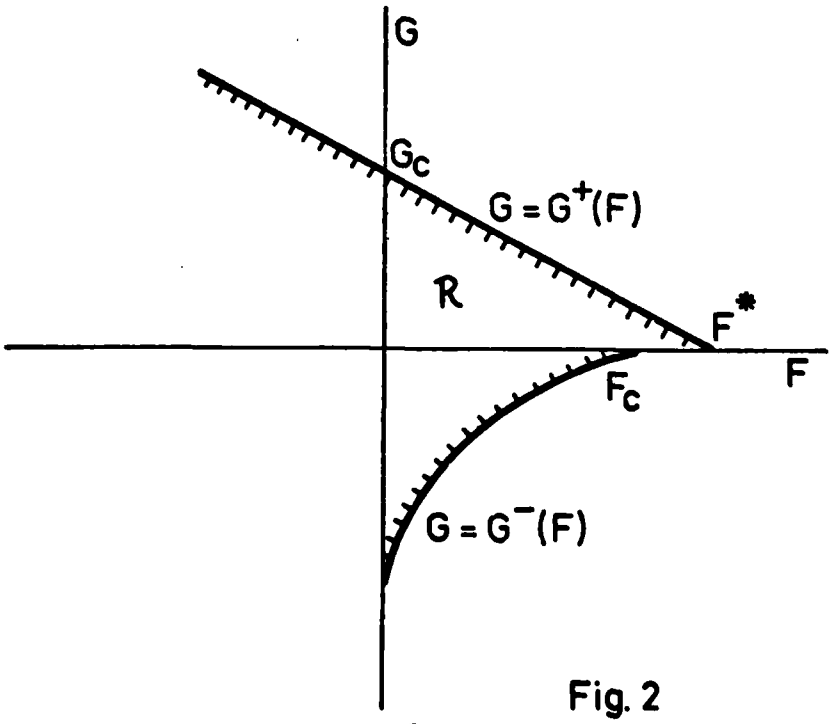


Fig. 2

As we have shown in our earlier work on harvesting of one species [Brauer and Soudack (1979a, 1979b)], the existence of an equilibrium in the interior of the first quadrant of the x-y plane does not guarantee the survival of both species. Resolution of this question depends not only on the existence of an equilibrium but also on the structure of separatrices at the one or more saddle points in the interior of the first quadrant. We have given a classification in the two one-species harvesting problems which can be combined into the following classification for any model of the form (1) with (F,G) in the interior of R, so that there is an equilibrium $P_\infty(F,G)$ in the interior of the first quadrant of the x-y plane. There is then at least one saddle point in the first quadrant, possibly on one of the axes.

Case 1. There is an orbit running from a saddle point as $t \to -\infty$ to P_∞ or a limit cycle around P_∞ as $t \to +\infty$.

Case 2. There is an orbit running from a saddle point as $t \to -\infty$ to a saddle point as $t \to +\infty$ (homoclinic-type orbit). The two saddle points may be the same.

Case 3. There is an orbit running from P_∞ or a limit cycle around P_∞ as $t \to -\infty$ to a saddle point as $t \to +\infty$.

For each case there are two alternatives which we index as a or b according as the equilibrium P_∞ is (locally) asymptotically stable or unstable respectively. In case 1a, P_∞ is asymptotically stable and there is a region of asymptotic stability for P_∞ - the set of initial values for which the solution tends to P_∞ as $t \to \infty$, which can be described in terms of the separatrices at saddle points. In case 1b, P_∞ is unstable but there is an asymptotically stable limit cycle with a domain of asymptotic stability which again can be described in terms of separatrices. Case 2 may be viewed as a transition between case 1 and case 3. In case 3a, P_∞ is asymptotically stable, but the domain of asymptotic stability consists only of the interior of an unstable periodic orbit around P_∞. In case 3b, P_∞ is unstable, and every orbit goes to an axis in finite time, corresponding to extinction of one of the species. Thus in practical terms, the two species can coexist only if the system is in case 1, even though in case 3a there is a

"small" set of initial values for which there is coexistence, and in case 2 there may be a coexistence region which is extremely susceptible to collapse under small perturbations of harvest rates.

This suggests the importance of dividing the region R in the F-G plane into subregions corresponding to the various cases in order to determine the set of values (F,G) for which the system can continue to function with both species co-existing. For any given $(F,G) \in R$, we may calculate $P_\infty(F,G)$, and then $\operatorname{tr} \Delta\{P_\infty(F,G)\}$. The set of points $(F,G) \in R$ for which $\operatorname{tr} \Delta\{P_\infty(F,G)\} = 0$ is a curve σ in R corresponding to the transition between the alternatives a and b (local asymptotic stability and instability respectively). There may be another curve h in R describing the set of values $(F,G) \in R$ for which there is a homoclinc type orbit and the system is in case 2. While the curve σ may be drawn approximately by calculation of $\operatorname{tr} \Delta\{P_\infty(F,G)\}$, the curve h can be approximated only by computer simulation of the orbits of the system (1) and classification of cases [Brauer and Soudack (1979a), (1979b)].

By examining the prey and predator isoclines it is not difficult to see that the qualitative structure for the system (1) with $F \neq 0$ is the same as the qualitative structure for the system (1) with $F = 0$, except that there are differences when $G = 0$ as shown in [Brauer and Soudack (1979b)]. By the same methods as those used in the case $F = 0$, we may establish the following results.

Theorem 1: There is a neighbourhood of the origin in the F-G plane in R for which the system (1) is in case 1a or in case 1b.

Theorem 2: If (F,G) is sufficiently close to the boundary of the region R in the F-G plane for which the system (1) has an equilibrium, and if $\operatorname{tr} \Delta\{P_\infty(F,G)\} \neq 0$, then the system (1) is in case 1a or in case 3b.

It follows from Theorem 2 that if the curve h goes to the boundary of R, it must intersect the curve σ there, since h can meet the boundary of R only in a point where $\operatorname{tr} \Delta\{P_\infty(F,G)\} = 0$. We have also shown [Brauer and Soudack (1980)] that in the third quadrant of the F-G plane, corresponding to stocking of both species, the system is in case 1a or case 1b. Thus the curve h can not enter the third quadrant.

A final general remark is that as we have shown in [Brauer and Soudack (1979b)], if the boundary $G = G^+(F)$ of R meets the F-axis at $(F_c,0)$ and the boundary $G = G^-(F)$ meets the F-axis at $(F^*,0)$ (Figure 1), then the system is in case 1a at $(F_c,0)$, while if $G = G^+(F)$ meets the F-axis at $(F^*,0)$ and $G = G^-(F)$ meets the F-axis at $(F_c,0)$, (Figure 2), then the system is in case 3b at $(F_c,0)$.

In the next section we shall indicate by considering a class of examples how the classifications for pure predator harvesting and pure prey harvesting can give information about the structure of the region R and the classification for two - species harvesting.

3. A Class of Examples

In our previous work on harvesting and stocking [Brauer, Soudack and Jarosch (1976); Brauer and Soudack (1979a), (1979b), (1980)], we have used the model

$$f(x,y) = r(1 - \frac{x}{K}) - \frac{y}{x+A}$$

(8)

$$g(x,y) = s(\frac{x}{x+A} - \frac{J}{J+A}) = \frac{sA(x-J)}{(J+A)(x+A)}$$

[Holling (1965)] as a source of examples. For this model, K and J are the K and J of the general theory in Section 2, while $L = rA$. As we have shown previously,

$$(9) \qquad G_c = \frac{rsA(K-J)^2}{4K(J+A)}, \quad F_c = \frac{rJ}{K}(K-J), \quad F^* = \frac{rK}{r} .$$

It is easy to calculate that

$$\text{tr } \Delta(x,y) = r(1 - \frac{2x}{K}) - \frac{Ay}{(x+A)^2} + \frac{sA(x-J)}{(J+A)(x+A)} .$$

In particular, if $F = G = 0$, then $x_\infty = J$, $y_\infty = \frac{r}{K}(J+A)(K-J)$, and

$$\text{tr } \Delta[x_\infty(0,0), y_\infty(0,0)] = \frac{rJ}{K(J+A)}(K-A-2J) .$$

For $F = F_c$ and $G = 0$, we have $x_\infty = J$, $y_\infty = 0$, and

$$\text{tr } \Delta[x_\infty(F_c,0), y_\infty(f_c,0)] = \frac{r}{K}(K-2J) .$$

For $F = 0$ and $G = G_c$, we have $x_\infty = \frac{J+K}{2}$, $y_\infty = \frac{r}{K}\frac{(J+K+2A)(K-J)}{4}$, and

$$\text{tr } \Delta[x_\infty(0,G_c), y_\infty(0,G_c)] = \frac{sAK(K-J)-r(A+J)^2(J+K)}{K(J+A)(2A+J+K)} .$$

The stability curve σ in the (F,G) plane corresponds to $\text{tr}\,\Delta = 0$. Thus for a given pair (F,G), we calculate $P_\infty(F,G)$, and hence $\text{tr}\,\Delta[P_\infty(F,G)]$. By varying (F,G) we may plot the curve σ. The curve h describing the pairs (F,G) for which there is a homoclinic orbit can not be sketched so easily. For this we need information about the dynamics of the system, and must compute orbits.

As we have observed in the general theory, there are situations in which we may have either predator extinction or prey extinction, depending on the initial state. We remark that it is easy to separate these two possibilities by computing the orbit from the origin in the x-y plane backwards in time. This orbit serves as a separatrix between predator extinction and prey extinction. (In practice, the computation may be carried out more efficiently if the starting point is taken near the origin rather than at the origin.

We now give several examples using this model to indicate the range of possibilities and the procedure for analyzing a model. For a given choice of the parameters of the model and a given pair of harvest rates, orbits can be approximated by computer simulation just as in our previous work [Brauer, Soudack and Jarosch (1976), Brauer and Soudack (1979a, 1979b, 1980)]. In this paper, we emphasize the shape and structure of the region R in the F-G plane for which there is an equilibrium in the interior of the first quadrant of the x-y plane, the curve σ in R corresponding to the transition between local asymptotic stability and instability of this equilibrium, and the curve h in R corresponding to values (F,G) for which there is a homoclinic type orbit. Thus we show orbits for only one of the examples, even though it is necessary to compute orbits in order to locate the curve h for every example. The curve σ and the boundary of the region R can be approximated numerically by calculation of equilibria and the trace of the matrix Δ, without requiring calculations of orbits. The computations reported below were carried out on the University of Wisconsin UNIVAC 1110 and the University of British Columbia Amdahl 470.

Our general procedure in each example has been to examine the case transitions as one of the harvest rates F,G is varied while the other is held at zero. This gives the "corners" of the region R. Then the boundary of R can be filled out by varying G

with F fixed. To locate the curves σ and h, we proceed just as we did in our previous work dealing with harvesting and stocking of a single species. For each example we make some general observations, not all of which are shown in the figures reproduced here.

Example 1: $r = 1$, $s = 1$, $A = 10$, $J = 20$, $K = 40$.

For this set of parameters, $F_c = F^* = 10$, $G_c = 0.8\overline{3}$, from (9). The system is in case 1a for all $(F,G) \in R$ (Figure 3) and is strongly stable in the sense that orbits approach the equilibrium $P_e(F,G)$ rapidly. The orbits are similar to those in the case of pure predator harvesting in that the stability region determined by the separatrices at the saddle point becomes smaller as G is increased. for each F. Outside the region of asymptotic stability, there is a region of prey extinction and a region of predator extinction which may be separated numerically by integration of the system backwards in time from $(\varepsilon,\varepsilon)$.

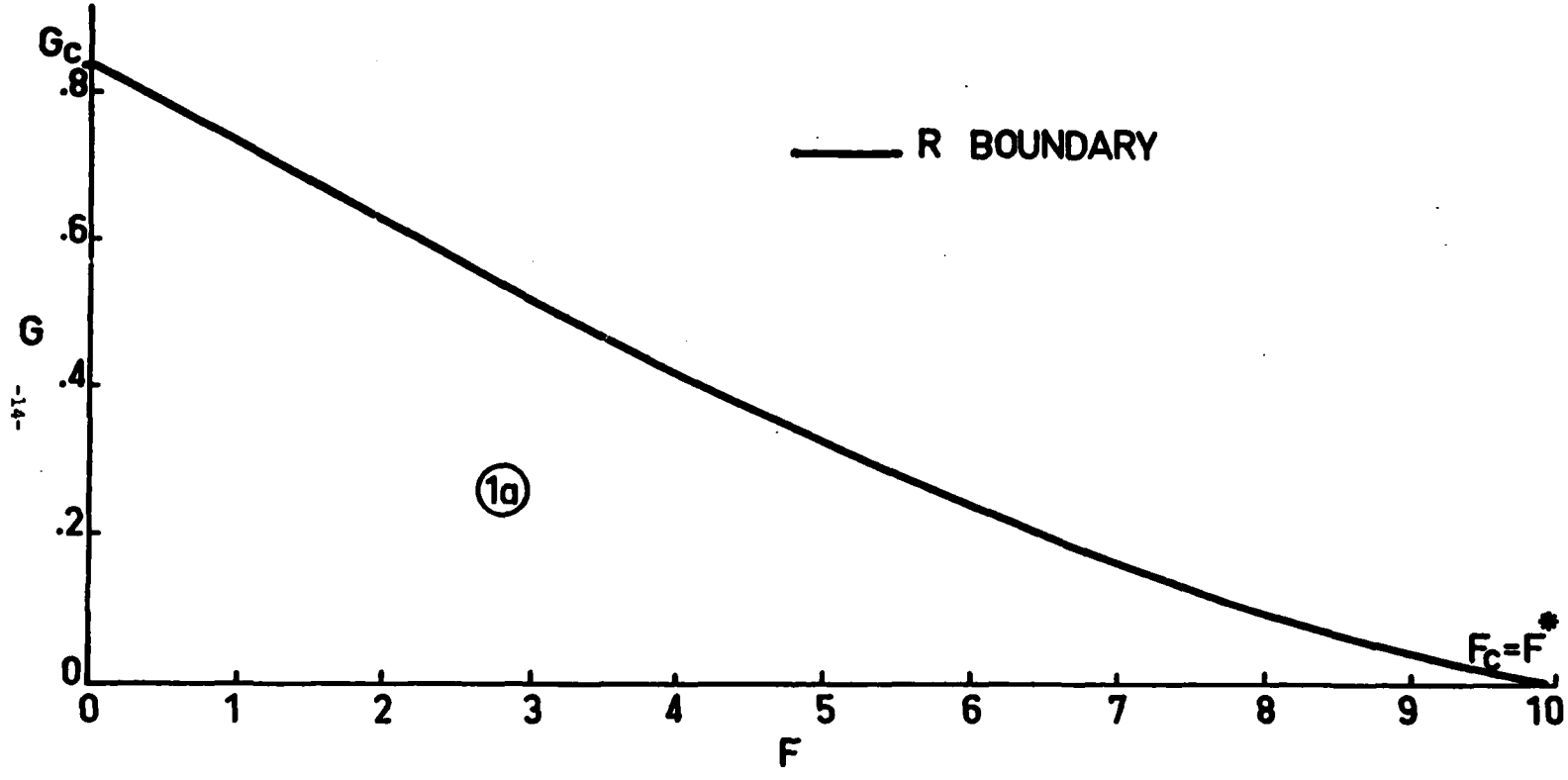


Fig. 3

Example 2: $r = 1$, $s = 4$, $A = 10$, $J = 20$, $K = 60$.

Here, $G_c = 8.8\overline{8}$, $F_c = 13.3\overline{3}$, $F^* = 15$, from (9). In both F and G separately, the case transitions are 1b → 2b → 3b (Figure 4). Note that since the equilibrium is unstable at $(F_c,0)$ the region R extends to $(F^*,0)$ in the first gradrant. As in Example 1, the region of asymptotic stability becomes smaller as G increases, and there is a coexistence region only for a small part of R.

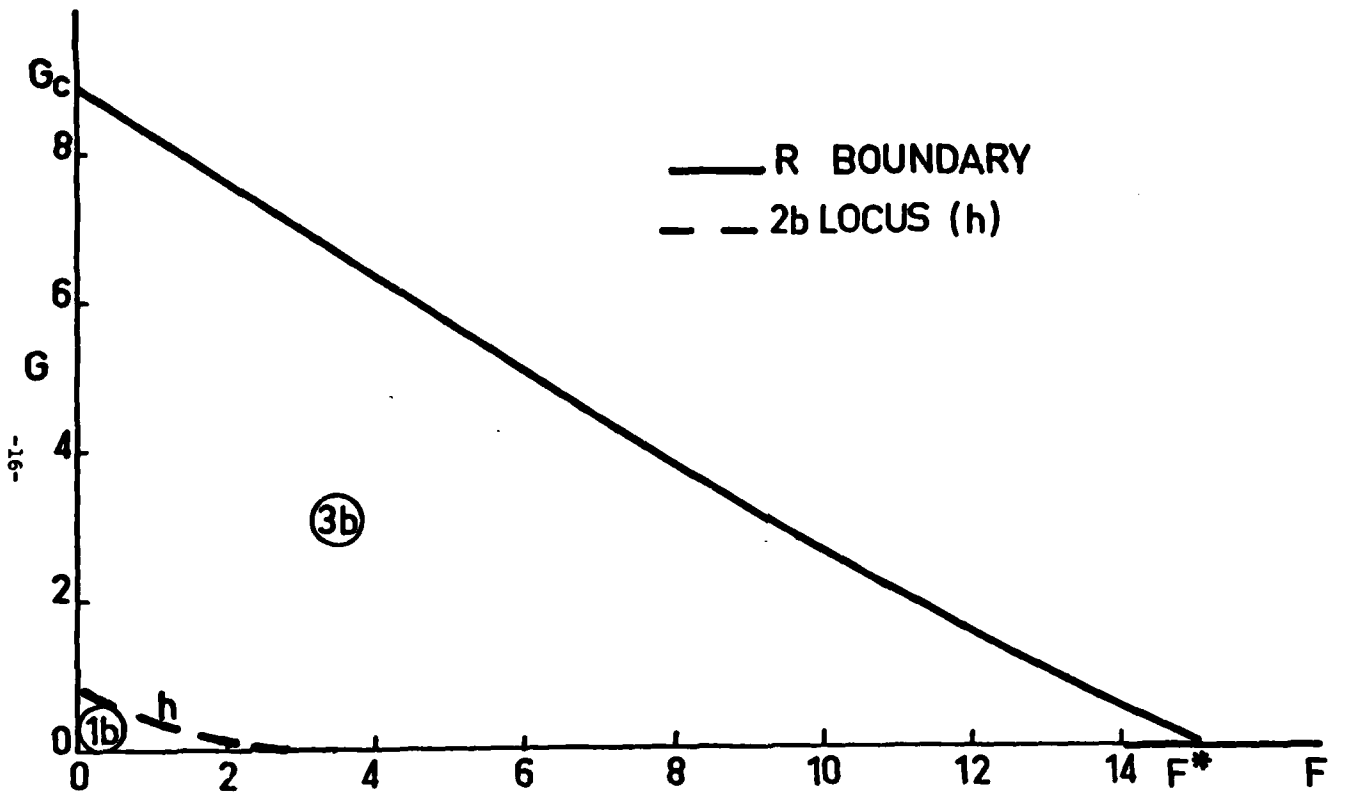


Fig. 4

Example 3: $r = 1$, $s = 7$, $A = 10$, $J = 20$, $K = 40$.

Here, $G_c = 5.8\overline{3}$, $F_c = F^* = 10$. The case transition is 1a → 2a → 3a → 3b in G for $F = 0$, and the system is in case 1a for $G = 0$, $0 < F < F^*$. The 3a region is very small, suggesting that in practical terms the transition is 1a → 3b. The system is weakly stable inn the sense that orbits approach the equilibrium P_∞ very slowly. For this example, we have also indicated the region R in all four quadrants of the F-G plane (Figure 5).

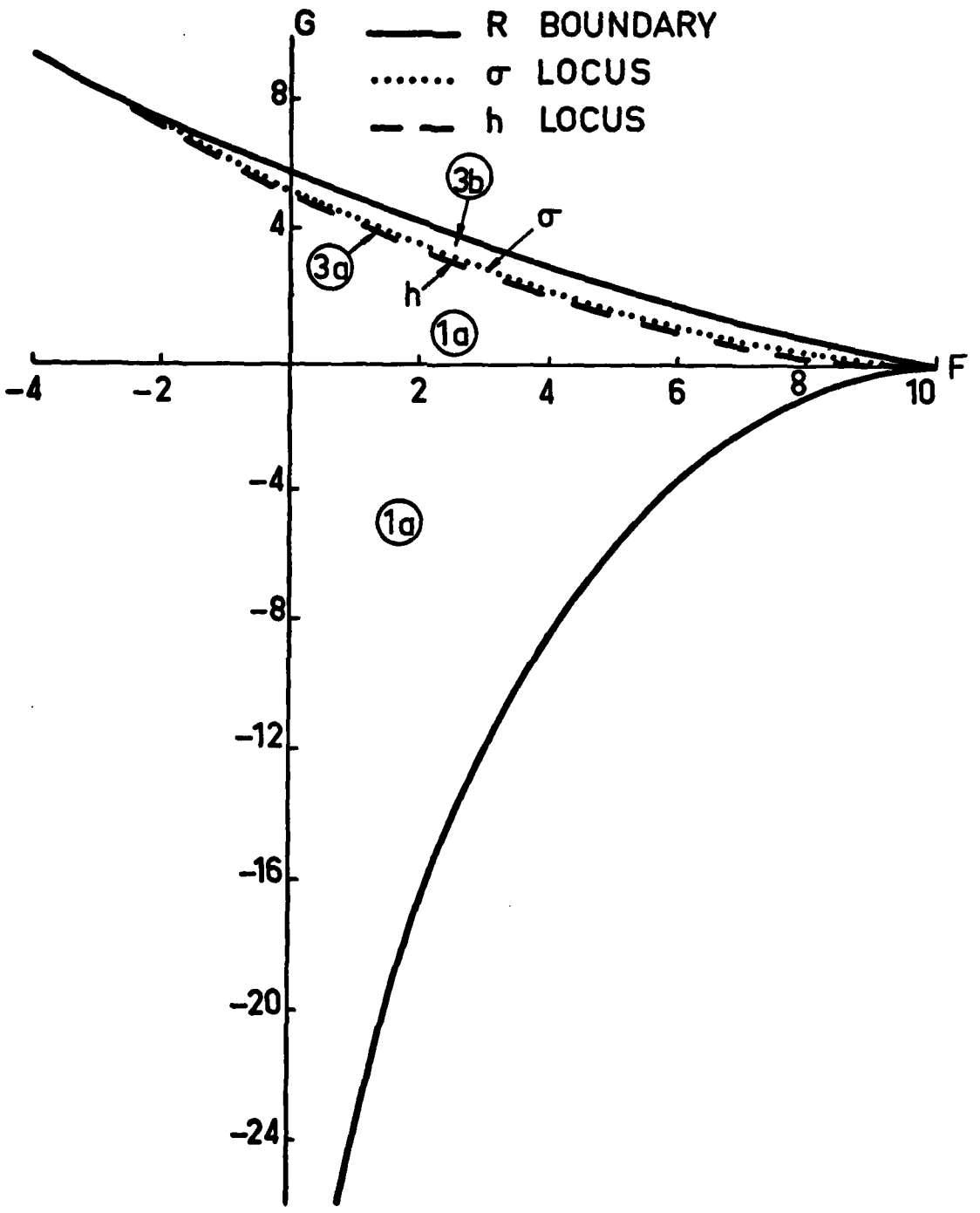

G
R BOUNDARY
σ LOCUS
h LOCUS
8
4
-4
-8
-12
-16
-20
-24
-4
-2
2
4
6
8
10
F
3b
σ
3a
h
1a
1a

Fig. 5

Example 4: $r = 1$, $s = 5$, $A = 10$, $J = 20$, $K = 45$.

Here, $G_c = 5.787$, $F_c = 11.1\overline{1}$, $F^* = 11.25$. The case transitions are 1a → 1b → 2b → 3b in F and 1a → 1b → 1a in G. Figure 6 indicates that the curves σ and h meet on the boundary of the region R. There are two components of the curve σ in the first quadrant; in Figure 6, we see how the curve σ goes into the second quadrant and then returns to the first quadrant, so that the two components are in the first quadrant are not really separate. The reader should note from Figure 6 that for fixed $F = 1$ and increasing G, the case transition is 1a → 1b → 2b → 3b → 2b → 1b → 1a; this is much more complicated than for $F = 0$, but can still be read from the figure.

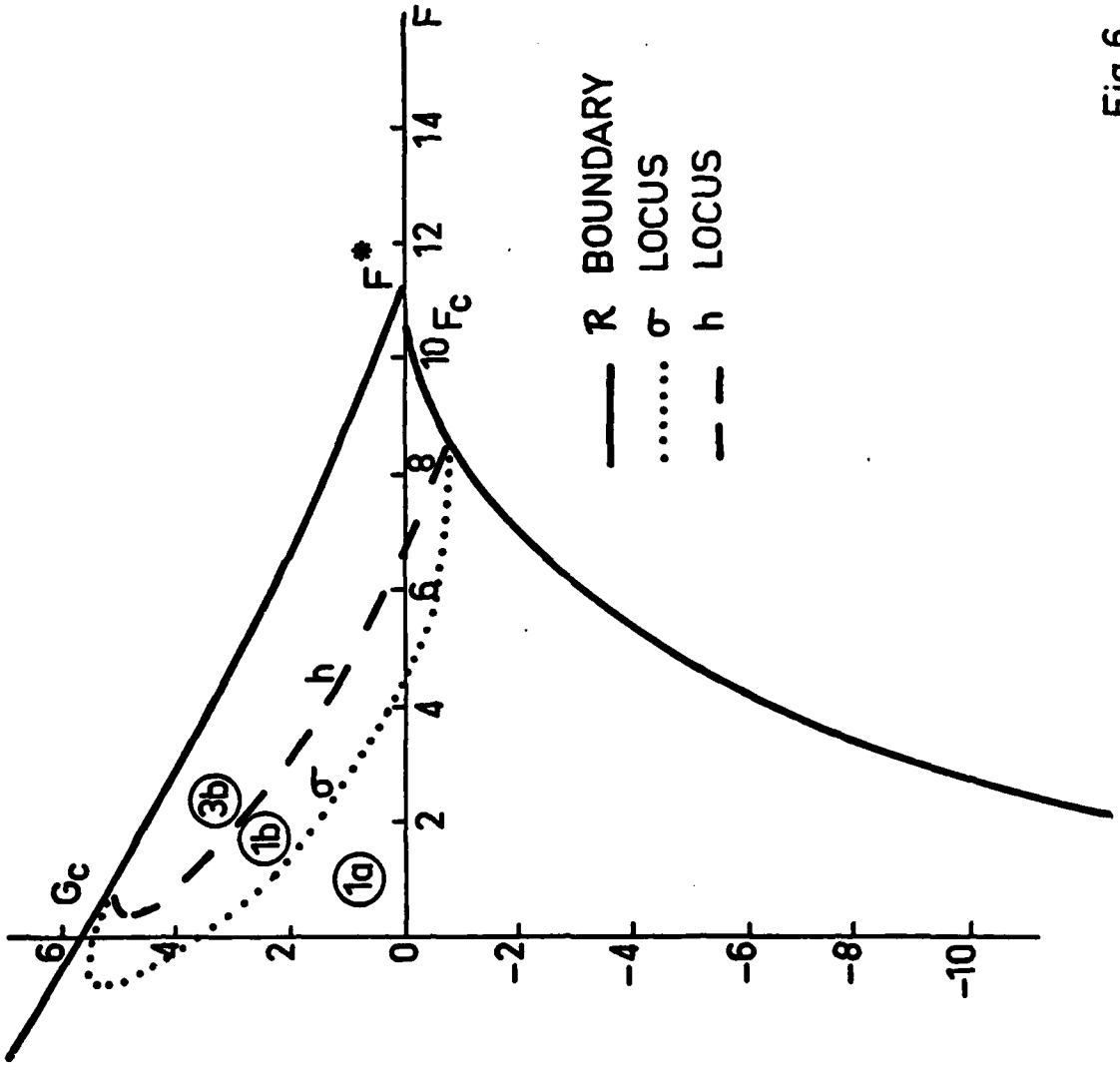

F
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
F*
Fc
Gc
-6
-4
2
R BOUNDARY
σ LOCUS
h LOCUS
1a
1b
3b
σ
h

Fig.6

Example 5: $r = 2$, $s = 1$, $A = 10$, $J = 20$, $K = 60$.

Here, $G_c = 4.44\overline{4}$, $F_c = 26.\overline{6}$, $F^* = 30$. The case transitions are 1b → 1a in G and 1b → 2b → 3b in F. Again, as may be seen, several transitions are possible when one of F and G is held fixed and the other is varied, more than in the special cases $F = 0$ and $G = 0$. We have included some phase portraits for this example. We see (Figure 7) that for $F = 3$, $G = 0.5$ the system is in case 3b. For $F = 3$, $G = 1$ (Figure 8) the system has just shifted to case 1b; the limit cycle is large with a further increase in G to $F = 3$, $G = 2$ (Figure 9) the system is still in case 1b but the limit cycle is smaller. For $F = 3$, $G = 3$ (Figure 10) the system is in case 1a. Note that in Figures 11, 12, 12, the separatrix between predator extinction and prey extinction is roughly the same but the region of coexistence shrinks as G increases even though P_∞ is stabilizing (locally). For larger F, $F = 13$, $G = 1.6$ (Figure 11) and $F = 13$, $G = 2$ (Figure 12) we have cases 1b and 1a respectively. The predator extinction - prey extinction separatrix is lower, giving a larger region of prey extinction and smaller regions of coexistence and predator extinction. In Figure 13, we have shown all four quadrants of the F-G plane, with the curves σ and h meeting at two points of the boundary of R. The 1b region in the fourth quadrant is unstable in practical terms because the limit cycles come very close to the coordinate axes. There is also a small 1a region in the fourth quadrant, but this also is not practically stable because P_∞ is very close to the y-axis.

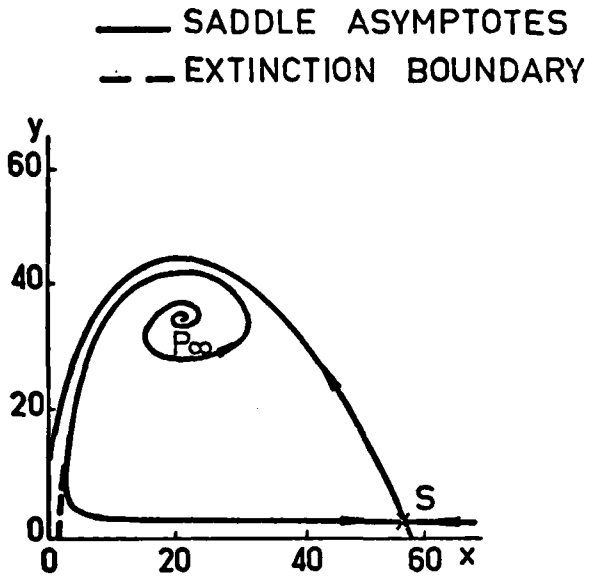

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
y
60
40
20
0
P_∞
S
0
20
40
60
x

Fig.7

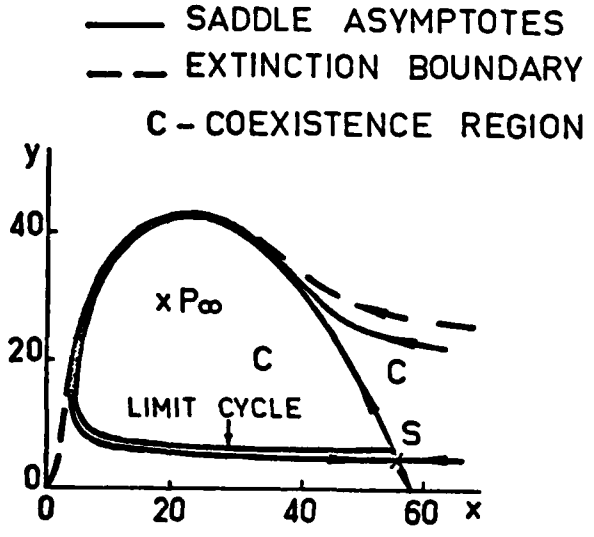

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
C - COEXISTENCE REGION
y
40
20
0
x P_∞
C
C
LIMIT CYCLE
S
0
20
40
60
x

Fig.8

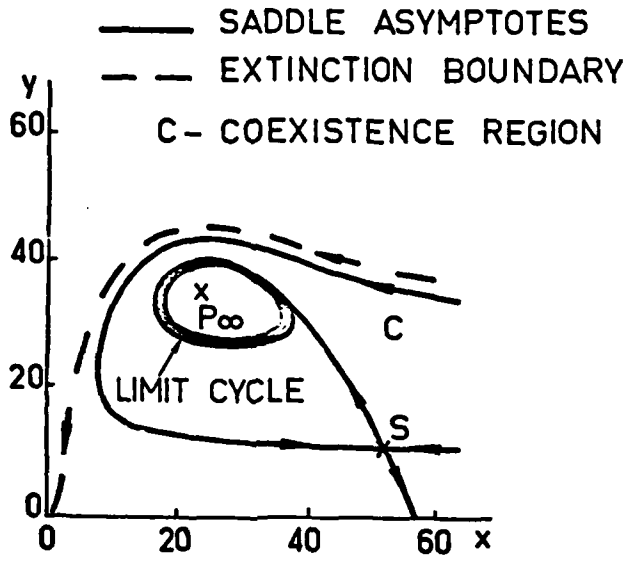

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
C - COEXISTENCE REGION
y
60
40
20
0
x
P∞
C
LIMIT CYCLE
S
0
20
40
60
x

Fig. 9

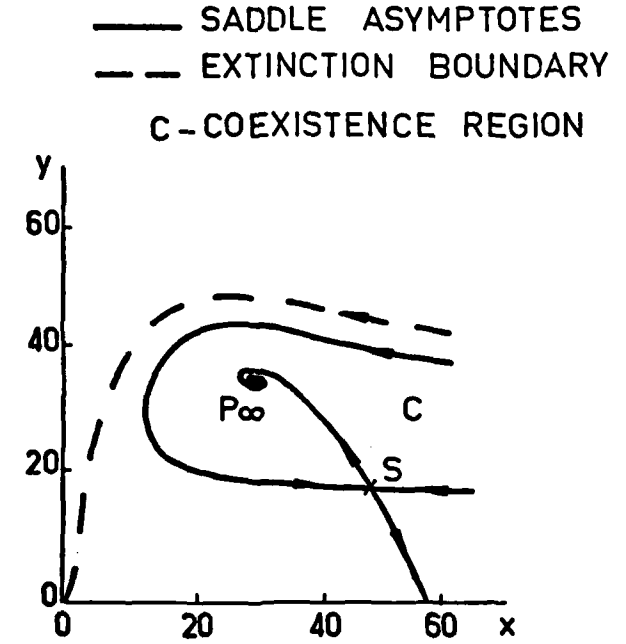

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
C - COEXISTENCE REGION
y
60
40
20
0
P∞
C
S
0
20
40
60
x

Fig.10

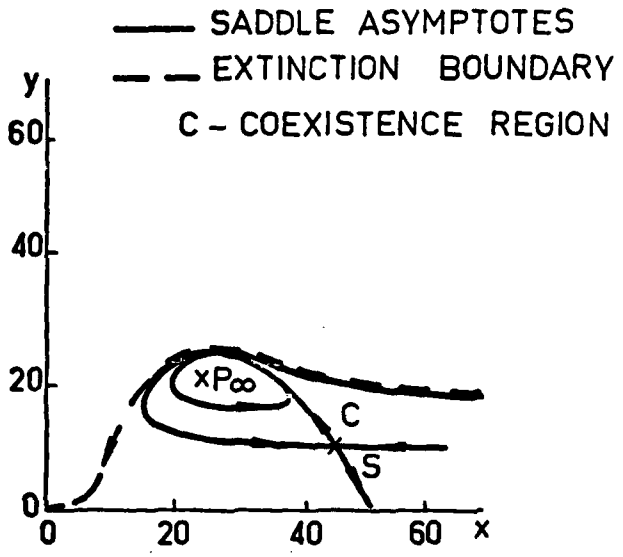

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
C - COEXISTENCE REGION
y
60
40
20
0
xP∞
C
S
0
20
40
60
x

Fig.11

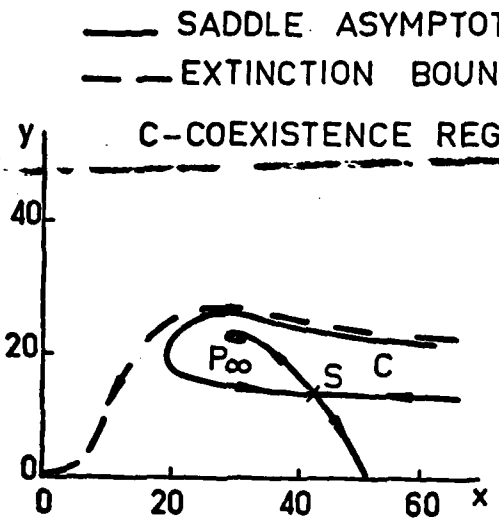

SADDLE ASYMPTOTES
EXTINCTION BOUNDARY
C-COEXISTENCE REGION
y
40
20
0
P∞
S
C
0
20
40
60
x

Fig.12

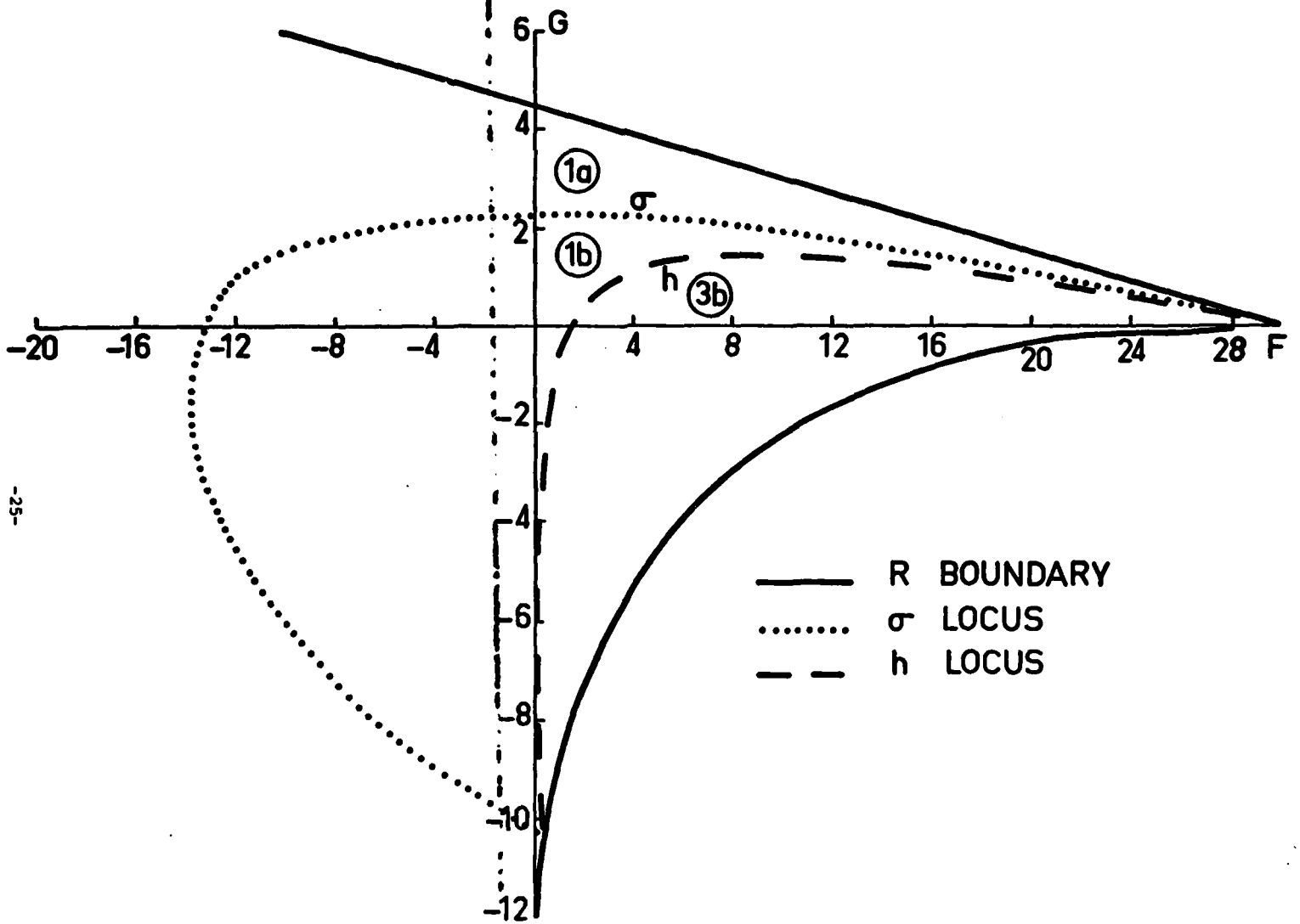

G
F
6
4
2
-2
-4
-6
-8
-10
-12
-20
-16
-12
-8
-4
4
8
12
16
20
24
28
1a
σ
1b
h
3b
R BOUNDARY
σ LOCUS
h LOCUS

Fig. 13

We have also examined some variations on Example 5, holding $r = 2$, $s = 1$, $A = 10$, $J = 20$ and changing K. For example, with $K = 50$, the curve σ passes through the origin (an immediate consequence of the fact that $K = 2J + A$). Qualitatively, the picture (Figure 14) is much like that for $K = 60$ (Figure 13), except that the curves σ and h have moved down. Similarly, for $K = 70$ the picture is similar except that the curves σ and h move upwards.

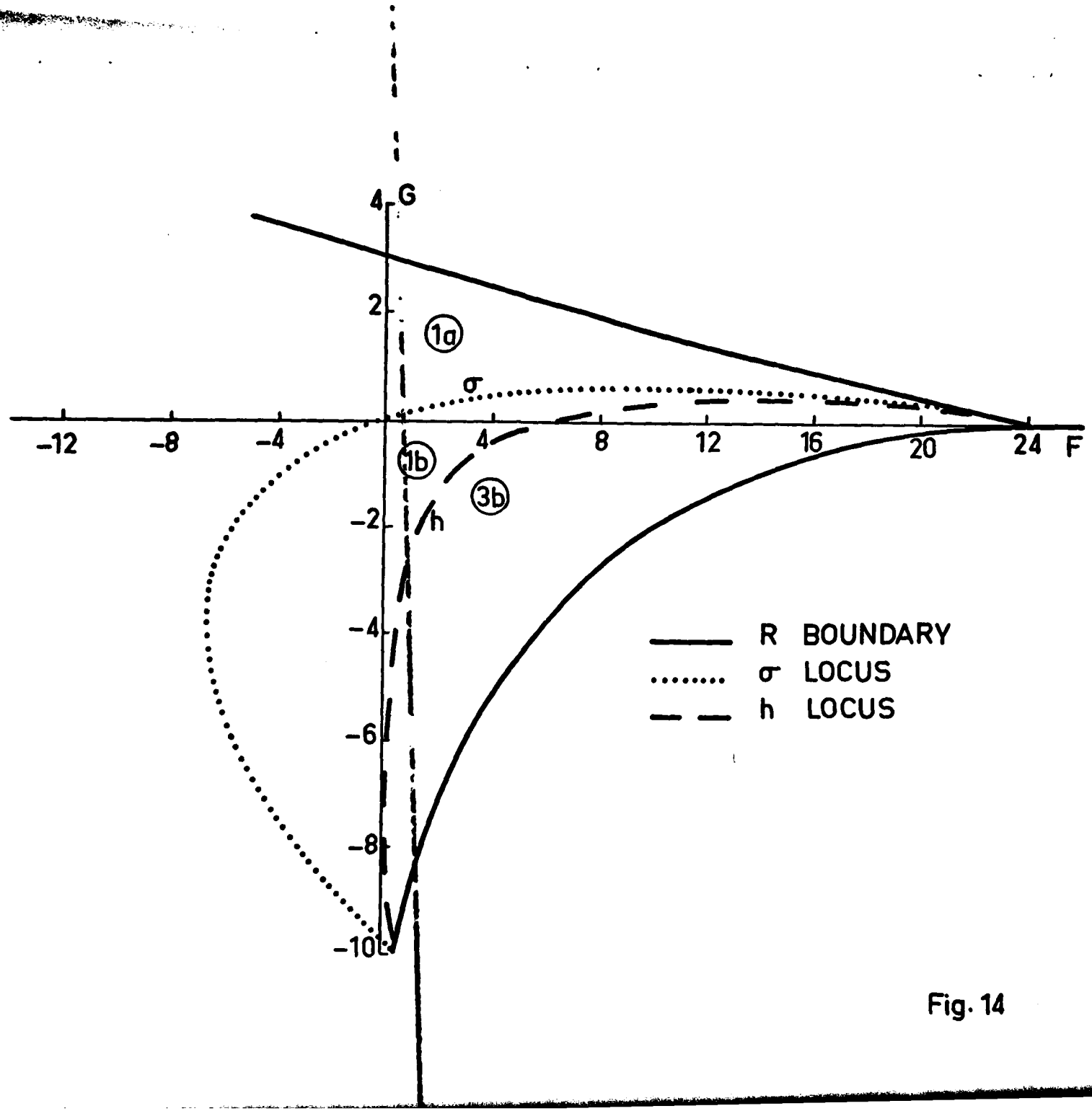

4
G
2
1a
σ
-12
-8
-4
1b
4
8
12
16
20
24
F
3b
h
-2
-4
-6
-8
-10
R BOUNDARY
σ LOCUS
h LOCUS

Fig. 14

4. Conclusions.

In this paper, we have generalized and completed the study of constant-rate harvesting and stocking in a class of idealized predator-prey systems. In general, the existence of a saddle point in the first quadrant of the phase plane causes the trajectories to be similar to those for predator harvesting alone rather than to prey harvesting alone (see References 2 and 3). There is however, one more transition trajectory separating the regions of predator extinction and prey extinction, as would be surmised.

Thus, we confined our attention to the F-G plane, and utilizing the fact of continuity across the F and G axes, we established a region R, for which P_∞ exists and loci σ and h which divide R into regions of stability, local instability, and no coexistence of species at all. The behaviour of the system, for all F and G, including all combinations of harvesting and stocking, is described by the loci in this plane.

One notable difference between two-species and one-species harvesting is that we no longer must stay in Case 3b once we get there. Increasing harvest rates might again establish coexistence regions. This phenomenon does not exist if either species is harvested separately.

The case of two-species stocking is not examined in detail here, since the results are given in [Brauer and Soudack, 1980]. It is enough to notice that the σ locus never enters the 3rd quadrant of the F-G plane and thus there is a region of coexistence for all stocking rates.

Examples where one specie is stocked and the other harvested, corresponding to the 2nd and 4th quadrants of the F-G plane, were considered, but the results are not included because the phase portraits are merely combinations of the cases for single specie harvesting and stocking. The relevant information is included in the description of the F-G plane.

Admittedly, there is some question regarding the idealized models considered in this study. However, studies of these idealized models have shown that the results obtained by linearization around equilibrium points are often incorrect and that such systems tend to

be much more fragile than expected, as far as coexistence is concerned. The next step is to consider more realistic harvesting strategies and to expand the models to include age and/or size structure.

The authors wish to thank Mr. Al MacKenzie of the Department of Electrical Engineering, University of British Columbia, for preparing the figures in this paper.

REFERENCES

1. F. Brauer, A. C. Soudack, H. S. Jarosch: Stabilization and destabilization of predator-prey systems under harvesting and nutrient enrichment, Int. J. Control 23, 553-573 (1976).
2. F. Brauer, A. C. Soudack: Stability regions and transition phenomena for harvested predator-prey systems, J. Math. Biology 7, 319-337, (1979).
3. F. Brauer, A. C. Soudack: Stability regions in predator-prey systems with constant-rate prey harvesting, J. Math. Biology 8, 55-71, (1979).
4. F. Brauer, A. C. Soudack: Constant-rate stocking of predator-prey systems, J. Math. Biology, to appear.
5. D. H. Griffel: Harvesting competing populations, Rocky Mountain J. of Math. 9, 87-91 (1979).
6. C. S. Hollig: The functional response of predators to prey density and its role in mimicry and population regulation, Mem. Ent. Soc. Canada 45, 1-73 (1965).
7. A. J. Reading: Models of competition between species: The effect of harvesting (unpublished).
8. P. Yodzis: The effects of harvesting on competitive species, Bull. Math. Biology 38, 97-109 (1976).

FB/ACS/jvs

LIST OF FIGURES

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER #2101	2. GOVT ACCESSION NO. AD-A089 639	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) COEXISTENCE PROPERTIES OF SOME PREDATOR-PREY SYSTEMS UNDER CONSTANT RATE HARVESTING AND STOCKING		5. TYPE OF REPORT & PERIOD COVERED Summary Report - no specific reporting period 6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s) F. Brauer and A. C. Soudack		8. CONTRACT OR GRANT NUMBER(s) DAAG29-80-C-0041 67-3138
9. PERFORMING ORGANIZATION NAME AND ADDRESS Mathematics Research Center, University of Wisconsin 610 Walnut Street Madison, Wisconsin 53706		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS Work Unit 1 - Applied Analysis
11. CONTROLLING OFFICE NAME AND ADDRESS U. S. Army Research Office P.O. Box 12211 Research Triangle Park, North Carolina 27709		12. REPORT DATE August 1980 13. NUMBER OF PAGES 31
14. MONITORING AGENCY NAME & ADDRESS(if different from Controlling Office)		15. SECURITY CLASS. (of this report) UNCLASSIFIED 15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)

Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Predator-prey systems, Harvesting, Stability

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

The global behaviour of a class of predator-prey systems, modelled by a pair of non-linear ordinary differential equations, under constant rate harvesting and/or stocking of both species, is presented. Theoretically possible structures and transitions are developed and validated by computer simulations. The results are presented as transition loci in the F-G (prey harvest rate - predator harvest rate) plane.

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE

UNCLASSIFIED

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)