

Coexistence Properties of Some Predator-Prey Systems Under Constant Rate Harvesting and Stocking*

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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.

Key words: Predator-prey systems – Harvesting – Stability

1. Introduction

In a sequence of papers [Brauer et al. (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 simultaneously. 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 what qualitative behaviour is to be expected under changes of one or both harvest rates. The models studied are oversimplified, but suggest unexpected dangers which may be relevant to the management of real-life systems if they persist in more realistic models.

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2. General Theory

We consider the system

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

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 et al. (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

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

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

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

As we have pointed out previously [Brauer and Soudack (1979a)], in many of the commonly-used models the 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

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

It is necessary to distinguish three possibilities, as follows:

- (i) $\alpha > 0$, corresponding to $f(0, 0) < 0$.
- (ii) $\alpha = 0$, corresponding to $f(0, 0) \geq 0$, 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 $J \geq K$ and $J \leq \alpha$ 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

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

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 $\text{tr} \Delta(\hat{P}) < 0$ and unstable if $\text{tr} \Delta(\hat{P}) > 0$ (corresponding to eigenvalues with negative real part and positive real part respectively).

If $G \neq 0$, the predator isocline $yg(x, y) = G$ 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 $xf(x, y) = F$ for $F \neq 0$, we define

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

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

or

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

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

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

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 quadrant 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 distinguish between the cases $F \geq 0$ 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 $0 \geq G > G^-$, 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 increasing 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 Figs. 1 and 2, the interior of the

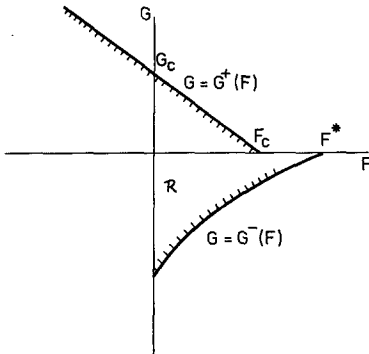


Fig. 1. $\alpha(F_c) < J, K(F_c) = J$

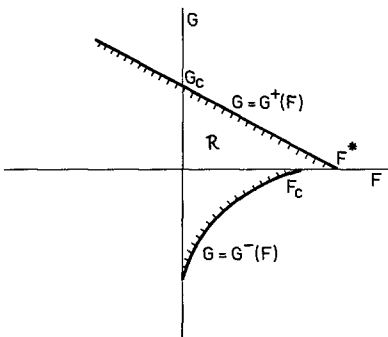


Fig. 2. $\alpha(F_c) = J, K(F_c) > J$

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)].

As we have shown in our earlier work on harvesting of one species [Brauer and Soudack (1979a and b)], 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 $t \rightarrow -\infty$ to P_∞ or a limit cycle around P_∞ as $t \rightarrow +\infty$.

Case 2. There is an orbit running from a saddle point as $t \rightarrow -\infty$ to a saddle point as $t \rightarrow +\infty$ (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 $t \rightarrow -\infty$ to a saddle point as $t \rightarrow +\infty$.

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 $t \rightarrow \infty$, 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 $\text{tr } \Delta\{P_\infty(F, G)\}$. The set of points $(F, G) \in R$ for which $\text{tr } \Delta\{P_\infty(F, G)\} = 0$ 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 homoclinic type orbit and the system is in case 2. While the curve σ may be drawn approximately by calculation of

$\text{tr } \Delta\{P_\infty(F, G)\}$, 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 $\text{tr } \Delta\{P_\infty(F, G)\} \neq 0$, 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 $\text{tr } \Delta\{P_\infty(F, G)\} = 0$. 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 cannot 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 $(F^*, 0)$ (Fig. 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 $(F_c, 0)$, (Fig. 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 et al. (1976); Brauer and Soudack (1979a), (1979b), (1980)], we have used the model

$$\begin{aligned} f(x, y) &= r \left(1 - \frac{x}{K} \right) - \frac{y}{x + A}, \\ g(x, y) &= s \left(\frac{x}{x + A} - \frac{J}{J + A} \right) = \frac{sA(x - J)}{(J + A)(x + A)} \end{aligned} \quad (8)$$

[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,

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

It is easy to calculate that

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

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

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

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

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

For $F = 0$ and $G = G_c$, we have

$$x_\infty = \frac{J+K}{2}, \quad y_\infty = \frac{r}{K} \frac{(J+K+2A)(K-J)}{4},$$

and

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

The stability curve σ in the (F, G) plane corresponds to $\operatorname{tr} \Delta = 0$. Thus for a given pair (F, G) , we calculate $P_\infty(F, G)$, and hence $\operatorname{tr} \Delta[P_\infty(F, G)]$. 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 cannot 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 et al. (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, $F_c = F^* = 10, G_c = 0.8\bar{3}$, from (9). The system is in case 1a for all $(F, G) \in R$ (Fig. 3) and is strongly stable in the sense that orbits approach the equilibrium $P_\infty(F, G)$ 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 $(\varepsilon, \varepsilon)$.

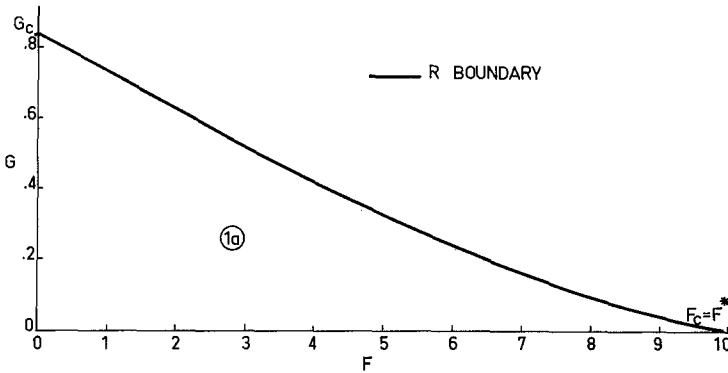


Fig. 3. $r = 1, s = 1, A = 10, J = 20, K = 40$

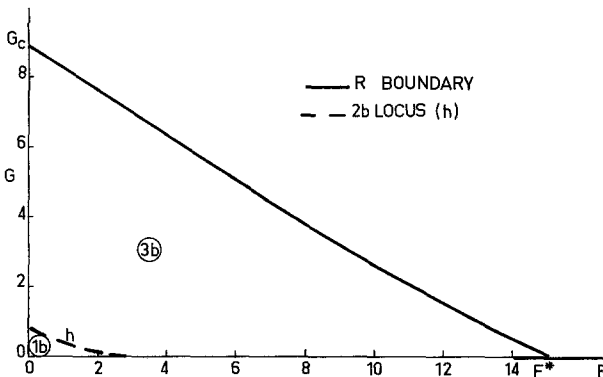


Fig. 4. $r = 1, s = 4, A = 10, J = 20, K = 60$

Example 2. $r = 1, s = 4, A = 10, J = 20, K = 60$. Here, $G_c = 8.8\bar{8}, F_c = 13.3\bar{3}, F^* = 15$, from (9). In both F and G separately, the case transitions are $1b \rightarrow 2b \rightarrow 3b$ (Fig. 4). Note that since the equilibrium is unstable at $(F_c, 0)$ the region R extends to $(F^*, 0)$ in the first quadrant. 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 .

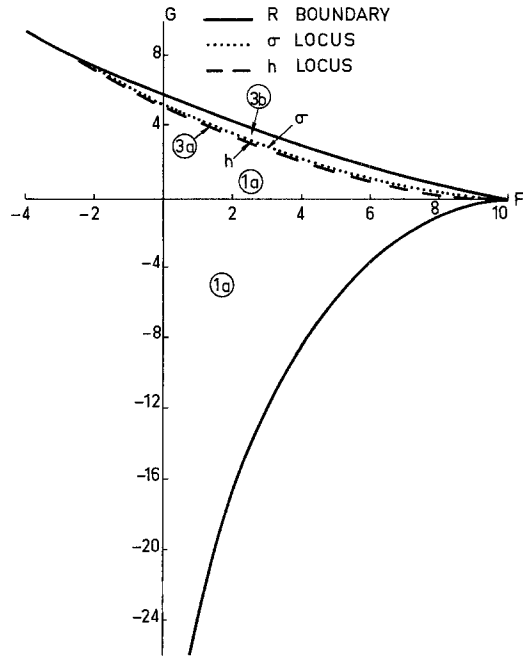


Fig. 5. $r = 1, s = 7, A = 10, J = 20, K = 40$ (full F - G plane)

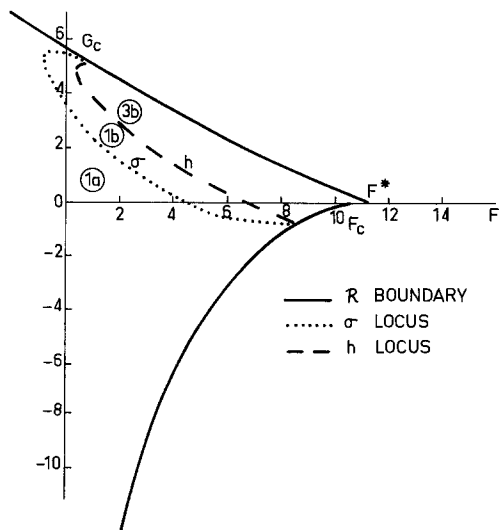


Fig. 6. $r = 1, s = 5, A = 10, J = 20, K = 45$ (full F - G plane)

Example 3. $r = 1, s = 7, A = 10, J = 20, K = 40$. Here, $G_c = 5.8\bar{3}, F_c = F^* = 10$. The case transition is $1a \rightarrow 2a \rightarrow 3a \rightarrow 3b$ in G for $F = 0$, and the system is in case 1a for $G = 0, 0 \leq F < F^*$. The 3a region is very small, suggesting that in practical terms the transition is $1a \rightarrow 3b$. The system is weakly stable in 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 (Fig. 5).

Example 4. $r = 1, s = 5, A = 10, J = 20, K = 45$. Here, $G_c = 5.787, F_c = 11.1\bar{1}, F^* = 11.25$. The case transitions are $1a \rightarrow 1b \rightarrow 2b \rightarrow 3b$ in F and $1a \rightarrow 1b \rightarrow 1a$ in G . Fig. 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 Fig. 6, we see how the curve σ goes into the second quadrant and then returns to the first quadrant, so that the two components in the first quadrant are not really separate. The reader should note from Fig. 6 that for fixed $F = 1$ and increasing G , the case transition is $1a \rightarrow 1b \rightarrow 2b \rightarrow 3b \rightarrow 2b \rightarrow 1b \rightarrow 1a$; this is much more complicated than for $F = 0$, but can still be read from the figure.

Example 5. $r = 2, s = 1, A = 10, J = 20, K = 60$. Here, $G_c = 4.4\bar{4}, F_c = 26.\bar{6}, F^* = 30$. The case transitions are $1b \rightarrow 1a$ in G and $1b \rightarrow 2b \rightarrow 3b$ 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 (Fig. 7) that for $F = 3, G = 0.5$ the system is in case 3b. For $F = 3, G = 1$ (Fig. 8) the system has just shifted to case 1b; the limit cycle is large with a further increase in G to $F = 3, G = 2$ (Fig. 9) the system is still in case 1b but the limit cycle is smaller. For $F = 3, G = 3$ (Fig. 10)

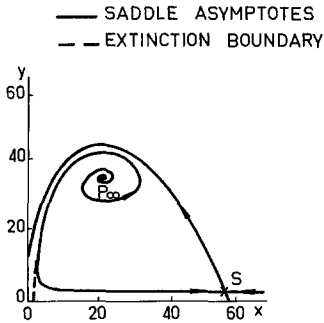


Fig. 7. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 3, G = 0.5$ (Case 3b)

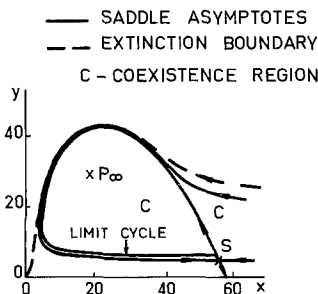


Fig. 8. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 3, G = 1$ (Case 1b)

Fig. 9. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 3, G = 2$
(Case 1b)

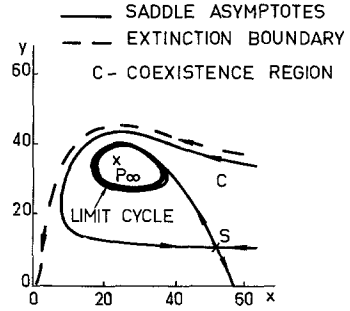


Fig. 10. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 3, G = 3$
(Case 1a)

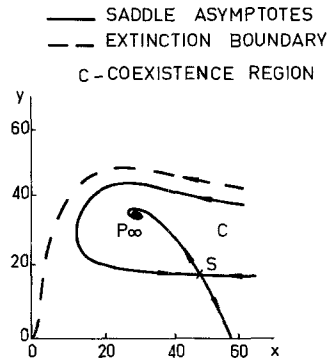


Fig. 11. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 13, G = 1.6$
(Case 1b)

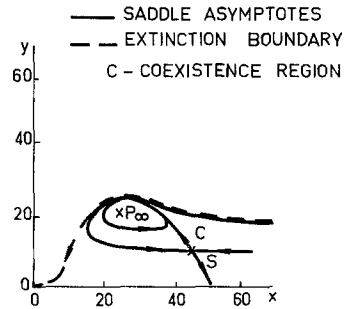
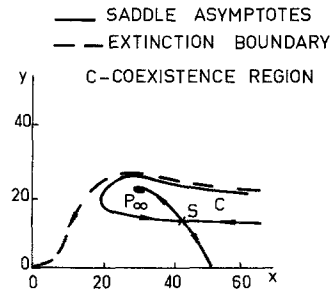


Fig. 12. $r = 2, s = 1, A = 10, J = 20, K = 60, F = 13, G = 2$
(Case 1a)



the system is in case 1a. Note that in Figs. 11, 12, 13, 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 , $F = 13$, $G = 1.6$ (Fig. 11) and $F = 13$, $G = 2$ (Fig. 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 Fig. 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

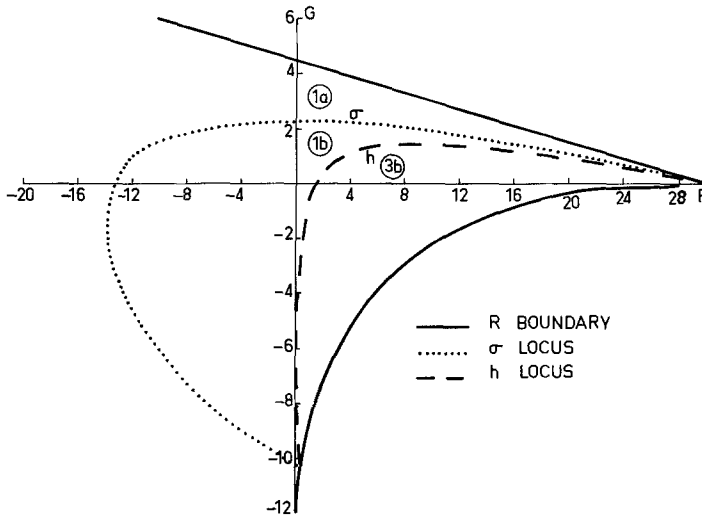


Fig. 13. $r = 2$, $s = 1$, $A = 10$, $J = 20$, $K = 60$ (full F - G plane)

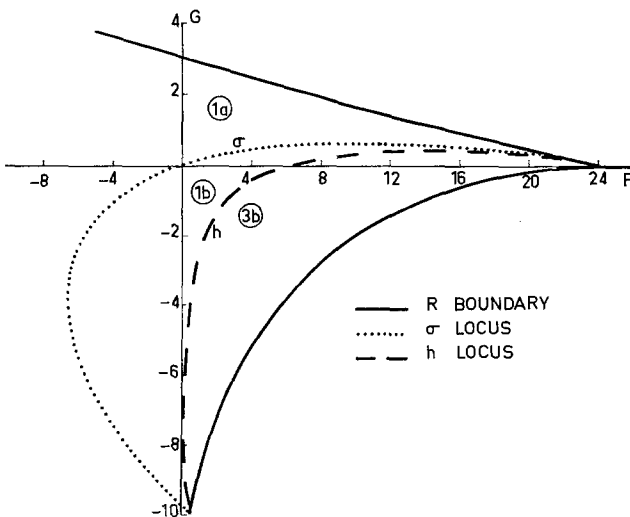


Fig. 14. $r = 2$, $s = 1$, $A = 10$, $J = 20$, $K = 50$ (full F - G plane)

fourth quadrant is unstable in practical terms because the limit cycles come very close to the coordinate axes. There is also a small Ia region in the fourth quadrant, but this also is not practically stable because P_∞ is very close to the y -axis.

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 (Fig. 14) is much like that for $K = 60$ (Fig. 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. Conclusions

We have extended the study of constant-rate harvesting in predator-prey systems to allow simultaneous harvesting of both species. This includes stocking of either or both species, viewed as negative harvesting. We have shown how to approximate the region of asymptotic stability in biological terms the initial states which lead to coexistence of the two species by efficient computer simulations. In situations where one of the two species must go to extinction, we have given a computational method of separating the initial states which lead to prey extinction from the initial states which lead to predator extinction. We have also shown how to identify values of the harvest rates for which the region of asymptotic stability disappears corresponding to collapse of the biological system for every initial state.

We illustrate our procedure by applying it to study of a class of examples. The results can be described by dividing the F - G plane, where F and G represent the prey and predator harvest rates respectively, into a region for which there is no equilibrium (extinction of one species), a region for which there is an asymptotically stable equilibrium (coexistence of both species in equilibrium), a region for which there is an asymptotically stable limit cycle (coexistence of both species in sustained oscillations), and a region for which there is an equilibrium but no region of asymptotic stability (extinction of one species). For any choice of the harvest rates we may use a computer simulation to estimate the region of coexistence if any.

The class of examples considered exhibits behaviour under harvesting of both species which cannot arise when only one species is harvested. A case in point is Example 5 for which if there is a positive prey harvest rate, an increase of the predator harvest may move the system from predator extinction to coexistence of both species. Such apparently paradoxical behaviour, if observable in real life, may be an indication of some external biological mechanism unrelated to the predators which is controlling the prey population.

Our primary point is that the results obtained by linearization about equilibrium points are often incorrect and that population systems tend to be much more fragile under harvesting than such analyses would suggest. These changes are not reduced in the more complex systems in which both systems are harvested. Whether still more complex systems with more realistic harvesting strategies continue to exhibit this fragility is a question deserving further study.

References

- Brauer, F., Soudack, A. C., Jarosch, H. S.: Stabilization and destabilization of predator-prey systems under harvesting and nutrient enrichment. *Int. J. Control* **23**, 553–573 (1976)
- Brauer, F., Soudack, A. C.: Stability regions and transition phenomena for harvested predator-prey systems. *J. Math. Biology* **7**, 319–337 (1979)
- Brauer, F., Soudack, A. C.: Stability regions in predator-prey systems with constant-rate prey harvesting. *J. Math. Biology* **8**, 55–71 (1979)
- Brauer, F., Soudack, A. C.: Constant-rate stocking of predator-prey systems. *J. Math. Biology* **11**, 1–14 (1981)
- Griffel, D. H.: Harvesting competing populations. *Rocky Mountain J. Math.* **9**, 87–91 (1979)
- Holling, C. S.: The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Ent. Soc. Canada* **45**, 1–73 (1965)
- Reading, A. J.: Models of competition between species: The effect of harvesting (unpublished data)
- Yodzis, P.: The effects of harvesting on competitive species. *Bull. Math. Biol.* **38**, 97–109 (1976)

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