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STABILITY REGIONS IN PREDATOR-PREY SYSTEMS WITH CONSTANT-RATE P--ETC(U)

JAN 79 F BRAUER, A C SOUDACK

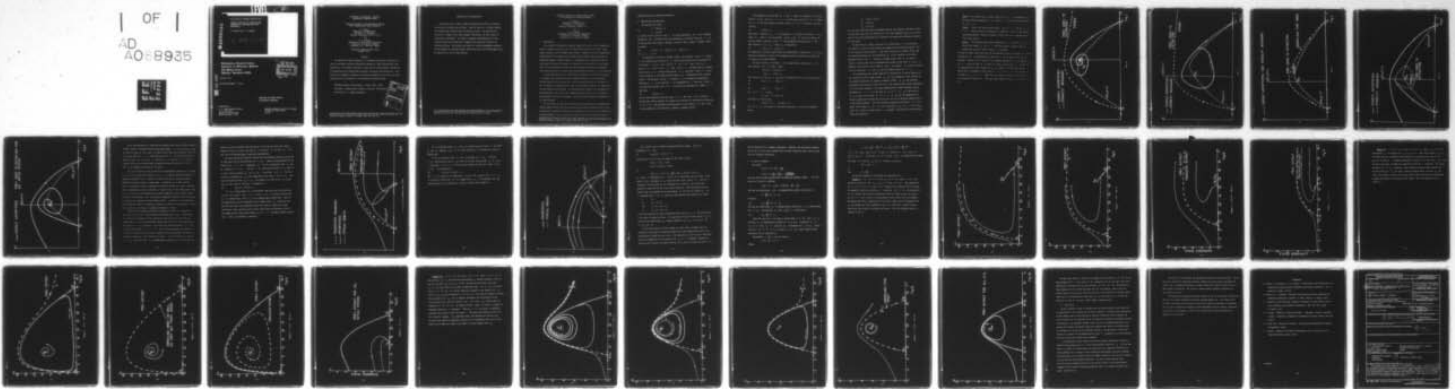
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STABILITY REGIONS IN PREDATOR-PREY SYSTEMS
WITH CONSTANT-RATE PREY HARVESTING

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Abstract

We analyze the global behavior of a predator-prey system, modelled by a pair of nonlinear ordinary differential equations, under constant-rate prey harvesting. By methods analogous to those used to study predator harvesting, we characterize the theoretically possible structures and transitions. With the aid of a computer simulation we construct examples to show which of these transitions can be realized in a biologically plausible model.

AMS(MOS) Subject Classification: 92A15, 34D05, 34C05

Key Words: predator-prey systems, stability, catastrophes.

Work Unit No. 1 - Applied Analysis

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Significance and Explanation

In previous work we have studied the qualitative effect of predator harvesting on predator-prey systems. Here we carry out a similar program for predator-prey systems under harvesting of prey. We find that the structure is simpler than under predator harvesting, but that there are significant differences. We obtain a complete characterization of the possible states and transitions, together with practical criteria for identifying them. The results are useful in resource management problems, giving methods for setting harvest rates which will avoid catastrophes such as extinction of one or both species.

The responsibility for the wording and views expressed in this descriptive summary lies with MRC, and not with the authors of this report.

STABILITY REGIONS IN PREDATOR-PREY SYSTEMS
WITH CONSTANT-RATE PREY HARVESTING

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1. Introduction

The study of differential equation models for predator-prey systems has been of interest since the work of Lotka (1924) and Volterra (1931); for a modern account, see for example [May (1976)]. Recently, we have analyzed the global behavior of predator-prey systems under constant-rate harvesting of predators [Brauer & Soudack (1979)]. The presence of a harvesting term implies that the region of asymptotic stability is not the entire first quadrant of the prey-predator plane, and we developed methods for determining this region as well as for describing the qualitative behavior of all solutions.

In this previous work, we indicated our intention of studying the effect of constant-rate harvesting of both predators and prey, with independent harvest rates for the two species. The underlying theoretical structure in this situation is essentially the same as for predator harvesting, unless only the prey species is harvested. For predator-prey systems under constant-rate prey harvesting, the results are somewhat different from those obtained for systems under constant-rate predator harvesting, even though the methods used are quite similar.

In this paper, we develop the theory of global behavior of predator-prey systems under constant-rate prey harvesting and show by examples which of the theoretically possible transitions can actually occur for a class of biologically motivated models. As in our previous work, some of the transitions can be

identified only by a computer simulation.

2. Theoretical Considerations

We consider the system

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

as a model for the sizes at time t of a prey population $x(t)$ and a predator population $y(t)$ from which prey are harvested at a constant time rate F . As in our previous work [Brauer, Soudack, & Jarosch (1976), Brauer & Soudack (1979)], we assume

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

for $x > 0, y > 0$.

As explained in [Brauer & Soudack (1979)], the equation $f(x,y) = 0$ defines y as a single-valued function of x , which we may assume to be non-negative on an interval $\alpha \leq x \leq K$, with $f(K,0) = 0$. If $\alpha = 0$, then $f(0,0) \geq 0$, while if $\alpha > 0$ and $f(\alpha,0) = 0$, then $f(0,0) < 0$. We shall draw all figures for the case $\alpha = 0$ in which there exists $L \geq 0$ such that $f(0,L) = 0$, which is the situation in the commonly-used models, e.g. [Rosenzweig (1971), Holling (1965)]. The equation $g(x,y) = 0$ defines x as a monotone non-decreasing function of y . If the function g is independent of y , the curve $g(x,y) = 0$ is a vertical straight line $x = J$. We assume the existence of a number $J > 0$ such that

$$(3) \quad g(J,0) = 0,$$

and we treat explicitly only the case $J < K$. (The case $J \geq K$ is easily analyzed by similar methods; the results are identical to those which we obtain for $J < K, F > F^*$. The biological interpretation of the numbers, J, K , and L , and of the assumptions are discussed in [Brauer & Soudack (1979)].

The assumptions we have made on f and g imply the existence of an intersection (x_∞, y_∞) with $x_\infty > 0$, $y_\infty > 0$ of the prey isocline for $F = 0$, namely $f(x, y) = 0$, and the predator isocline $g(x, y) = 0$. As F increases, the prey isocline

$$(4) \quad xf(x, y) = F$$

moves down (because $f_y < 0$, an increase in F implies a decrease in y for fixed x). There is an intersection $[x_\infty(F), y_\infty(F)]$ of the prey isocline (4) and the predator isocline $g(x, y) = 0$ which depends continuously on F for some interval $0 \leq F \leq F_C$, where F_C is defined by

$$(5) \quad x_\infty(F_C) = J, \quad y_\infty(F_C) = 0.$$

For simplicity, we shall assume that this intersection is unique for $0 \leq F \leq F_C$. There are situations in which this assumption could be violated, but these can be treated by the same methods.

The prey isocline (4) defines y as a single-valued function of x on some interval $\alpha(F) \leq x \leq \beta(F)$, where

$$f\{\alpha(F), 0\} = f\{\beta(F), 0\} = F$$

$$\alpha(0) = \alpha, \quad \beta(0) = K.$$

The critical prey harvest F_C may also be characterized by the fact that either

$$(5) \quad \alpha(F_C) < J, \quad \beta(F_C) = J$$

or

$$(6) \quad \alpha(F_C) = J, \quad \beta(F_C) > J.$$

For $0 \leq F < F_C$, we have

$$0 \leq \alpha(F) < J < \beta(F) \leq K,$$

from which it follows that

$$g\{\alpha(F), 0\} < 0, \quad g\{\beta(F), 0\} > 0.$$

For $0 \leq F < F_C$, the system (1) has three equilibria in the first quadrant, namely

$$P_{\infty} = [x_{\infty}(F), y_{\infty}(F)]$$

$$S_{\alpha} = [\alpha(F), 0]$$

$$S_{\beta} = [\beta(F), 0] .$$

This is quite different from the predator-harvest case [Brauer & Soudack (1979)], in which there are only two equilibria in the first quadrant, and it is the presence of the third equilibrium which produces the qualitative differences between the two cases.

We may study the (local) stability of an equilibrium P by linearizing the system (1) about the equilibrium and examining the coefficient matrix $A(P)$ of the resulting linear system. It has been pointed out by Bulmer (1976) that the assumed uniqueness of the equilibrium P_{∞} in the interior of the first quadrant implies that P_{∞} cannot be a saddle point. Thus P_{∞} is either a node or a spiral point, and is asymptotically stable if the trace of $A(P_{\infty})$ is negative, and unstable if the trace of $A(P_{\infty})$ is positive. It is easy to verify that the equilibria S_{α} and S_{β} are both saddle points for $F < F_c$.

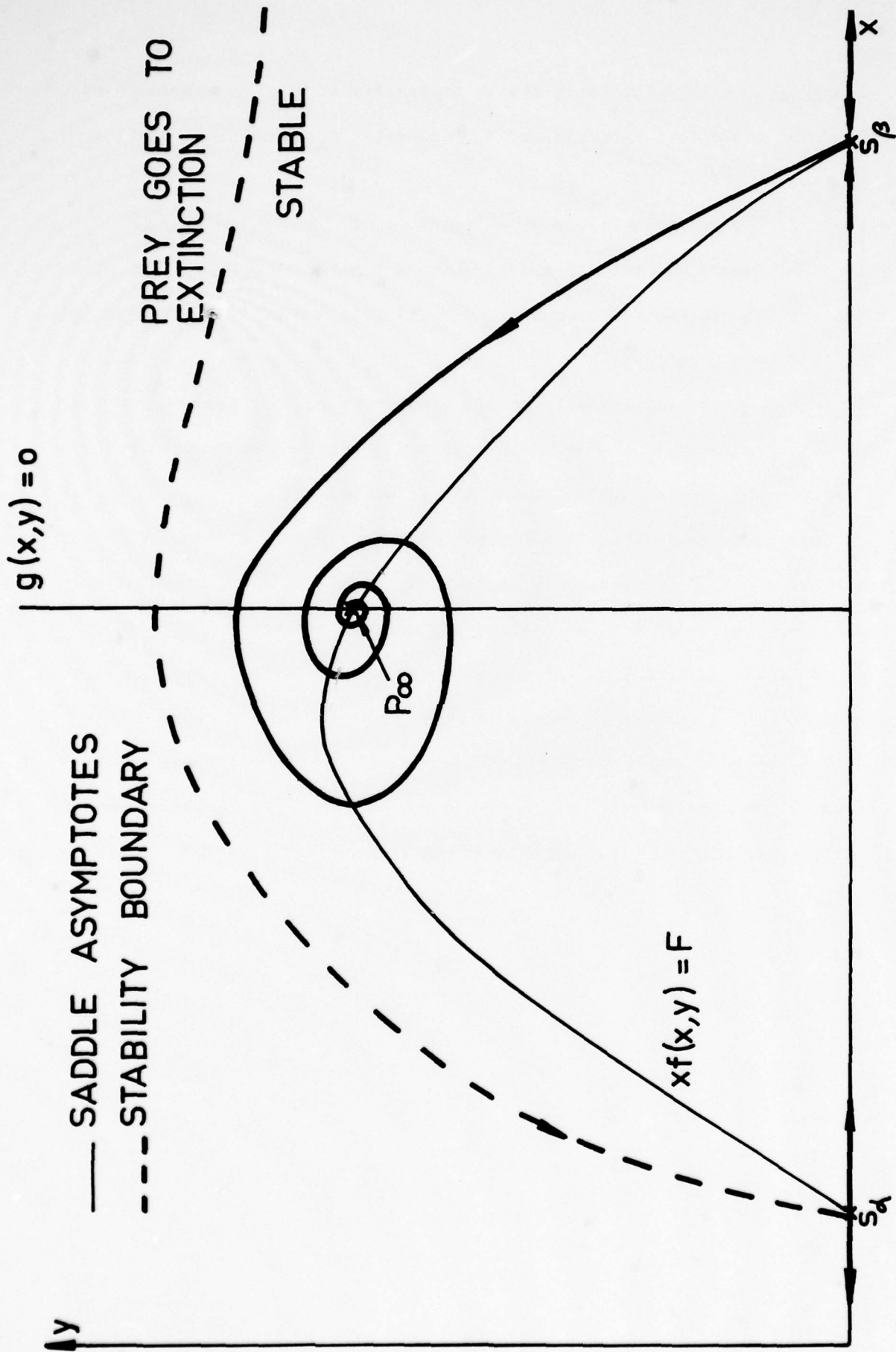
We may determine the global behavior of solutions of (1) by an analysis of the separatrices at the saddle points S_{α} and S_{β} analogous to that carried out for predator harvesting in [Brauer & Soudack (1979)]. At S_{α} , the unstable separatrices are along the x-axis and one of the asymptotically stable separatrices is in the fourth quadrant. The other asymptotically stable separatrix may be unbounded as $t \rightarrow -\infty$, or it may tend to S_{β} as $t \rightarrow -\infty$, or it may tend to P_{∞} or a limit cycle around P_{∞} as $t \rightarrow -\infty$. At S_{β} , the two asymptotically stable separatrices are along the x-axis and one of the unstable separatrices is in the fourth quadrant. The other unstable separatrix may tend to P_{∞} or to a limit cycle around P_{∞} as $t \rightarrow \infty$, or it may tend to S_{α} as $t \rightarrow \infty$, or it may reach the y-axis in finite time as t increases. We are led to the following three possibilities:

Case 1: The asymptotically stable separatrix at S_α is unbounded as $t \rightarrow -\infty$ and the unstable separatrix at S_β tends to P_∞ or a limit cycle around P_∞ as $t \rightarrow \infty$.

Case 2: There is an orbit which tends to S_α as $t \rightarrow \infty$ and to S_β as $t \rightarrow -\infty$. (Such an orbit is analogous to a homoclinic orbit in the predator harvesting problem [Brauer & Soudack (1979)], and will be called a homoclinic type orbit.)

Case 3: The asymptotically stable separatrix at S_α tends to P_∞ or a limit cycle around P_∞ as $t \rightarrow -\infty$, and the unstable separatrix at S_β reaches the y-axis in finite time as t increases.

For each of these cases there are two alternatives, which we index as a if the equilibrium P_∞ is asymptotically stable and b if the equilibrium P_∞ is unstable. Observe that in case 1a, the unstable separatrix at S_β tends to P_∞ as $t \rightarrow \infty$ while in case 1b it tends to a limit cycle around P_∞ . In case 3a, the asymptotically stable separatrix at S_α tends to a limit cycle around P_∞ (which must be unstable on both sides as $t \rightarrow \infty$) as $t \rightarrow -\infty$, while in case 3b it tends to P_∞ as $t \rightarrow -\infty$. There are five types of possible phase portraits, as indicated in Figures 1-5. (The same figure describes both case 2a and case 2b.)



— SADDLE ASYMPTOTES
 - - - STABILITY BOUNDARY

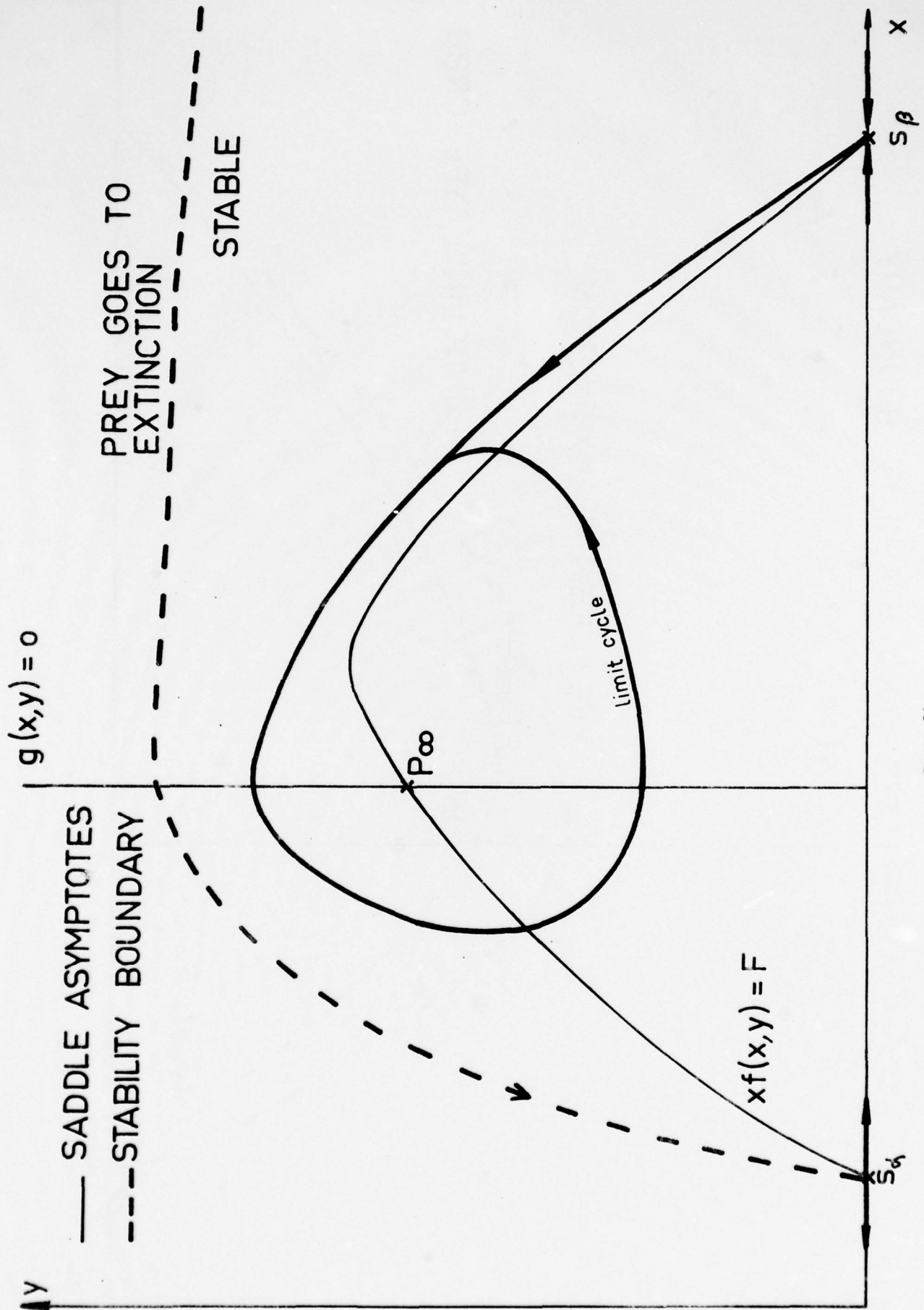
PREY GOES TO
 EXTINCTION

STABLE

$xf(x,y) = F$

Case 1a.

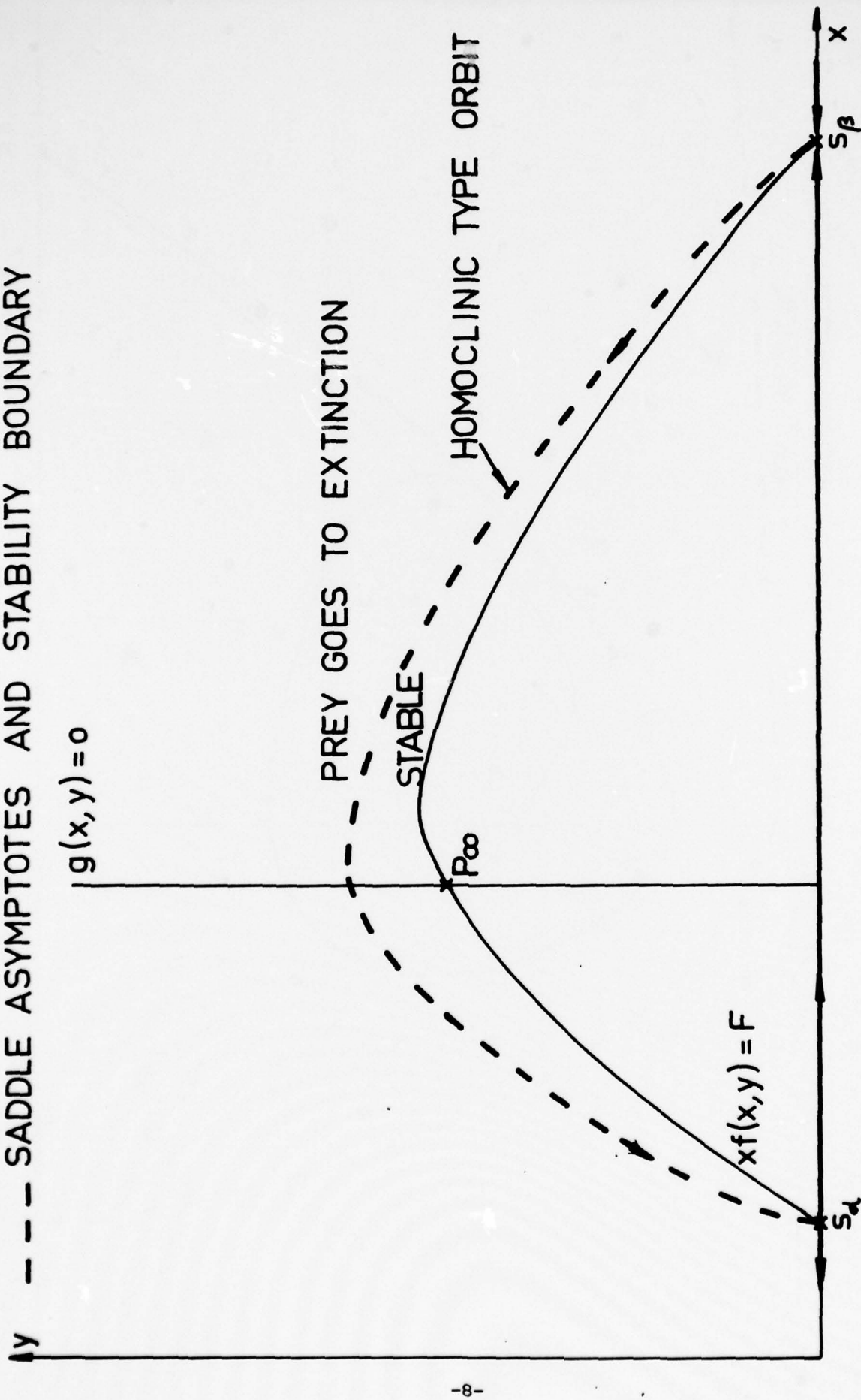
Fig. 1



Case 1b.

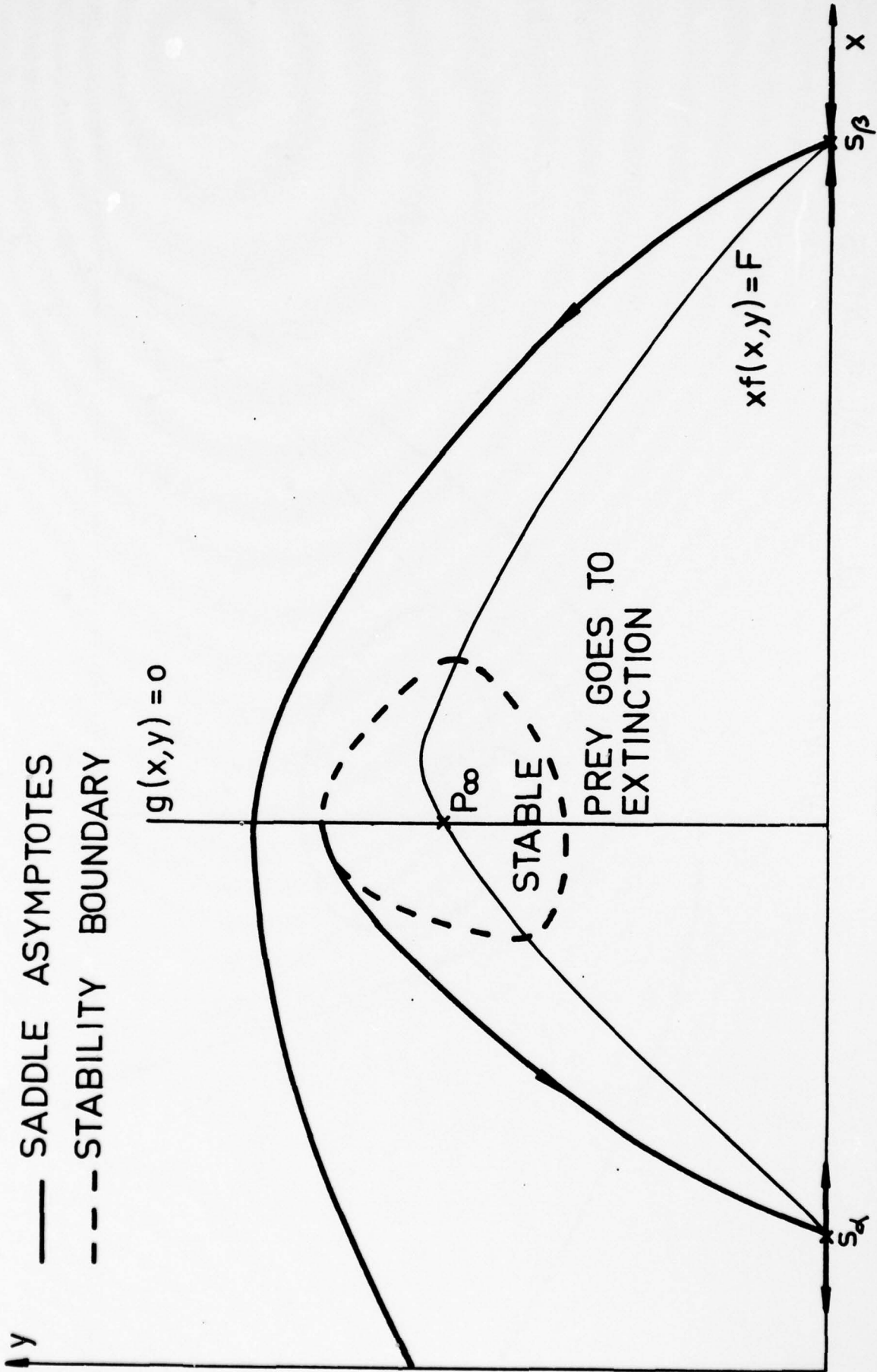
Fig. 2

--- SADDLE ASYMPTOTES AND STABILITY BOUNDARY



Case 2.

Fig.3

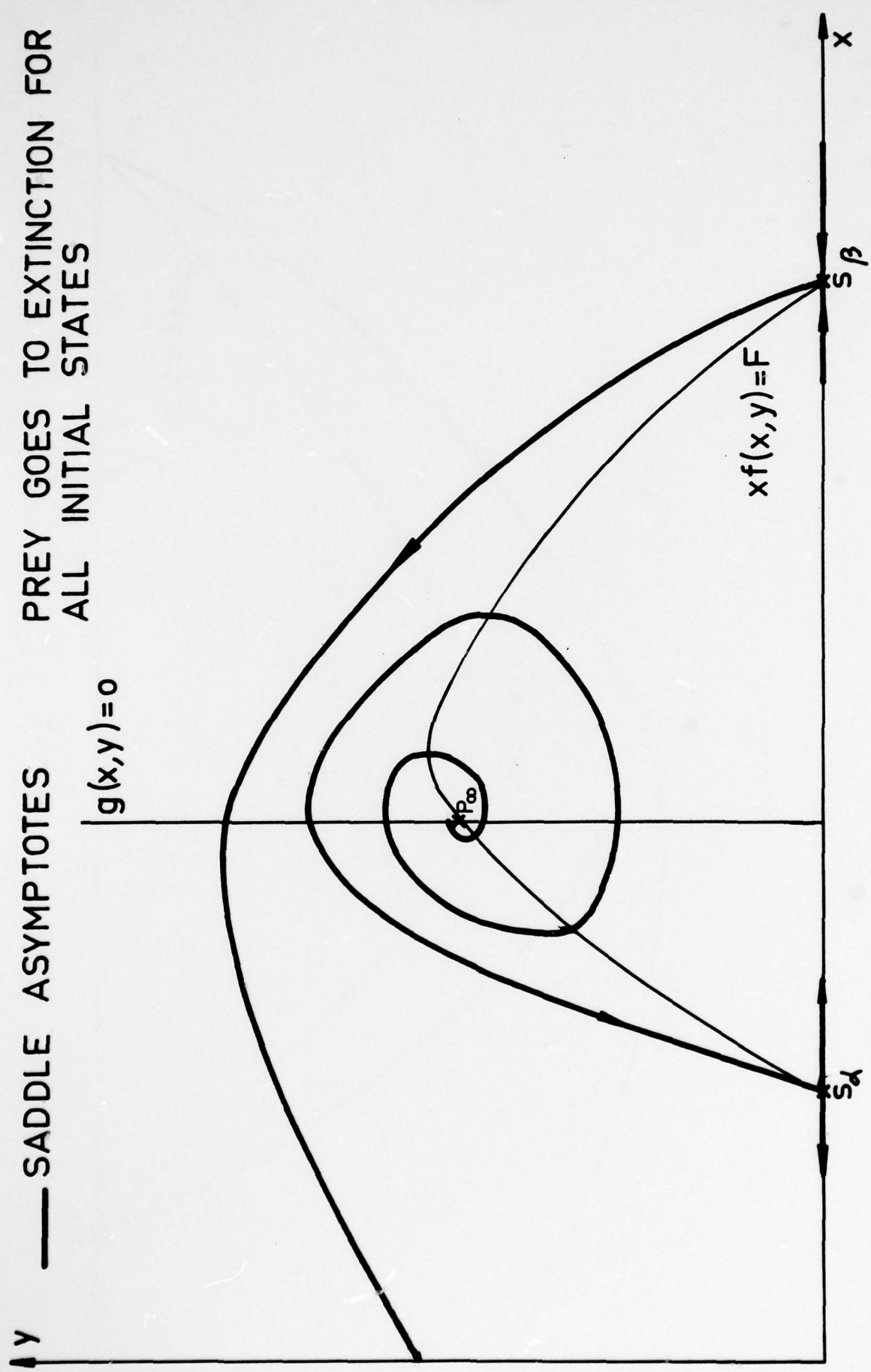


Case 3a.

Fig.4

— SADDLE ASYMPTOTES

PREY GOES TO EXTINCTION FOR ALL INITIAL STATES



Case 3b.

Fig.5

By the same arguments as those for the predator harvesting situation [Brauer & Soudack (1979)], we may prove that for sufficiently small $F \geq 0$ the system (1) must be either in case 1a or in case 1b, while if the trace of the matrix $A[P_\infty(F_C)]$ is non-zero then for $F < F_C$ sufficiently close to F_C the system (1) must be either in case 1a or in case 3b. Both for $F \rightarrow 0$ and for $F \rightarrow F_C$, the two possibilities can be distinguished by checking the local stability of $P_\infty(F)$, that is, by computing the trace of $A[P_\infty(F)]$.

The set of initial values for which the corresponding solution of (1) tends to P_∞ or to a limit cycle around P_∞ as $t \rightarrow +\infty$ may be called the region of asymptotic stability of (i), since it is the set of initial states for which predators and prey co-exist in some sense. A solution of (1) whose initial value is outside the region of asymptotic stability reaches the y-axis in finite time, corresponding to prey extinction, or tends to one of the saddle points (but only if it is one of the asymptotically stable separatrices at the saddle point). In each of the possible cases, the region of asymptotic stability can be described in terms of the separatrices at the saddle points. In Figures 1-5 the separatrix which bounds the region of asymptotic stability is shown as a dashed line. Observe that in case 3b, the region of asymptotic stability is empty.

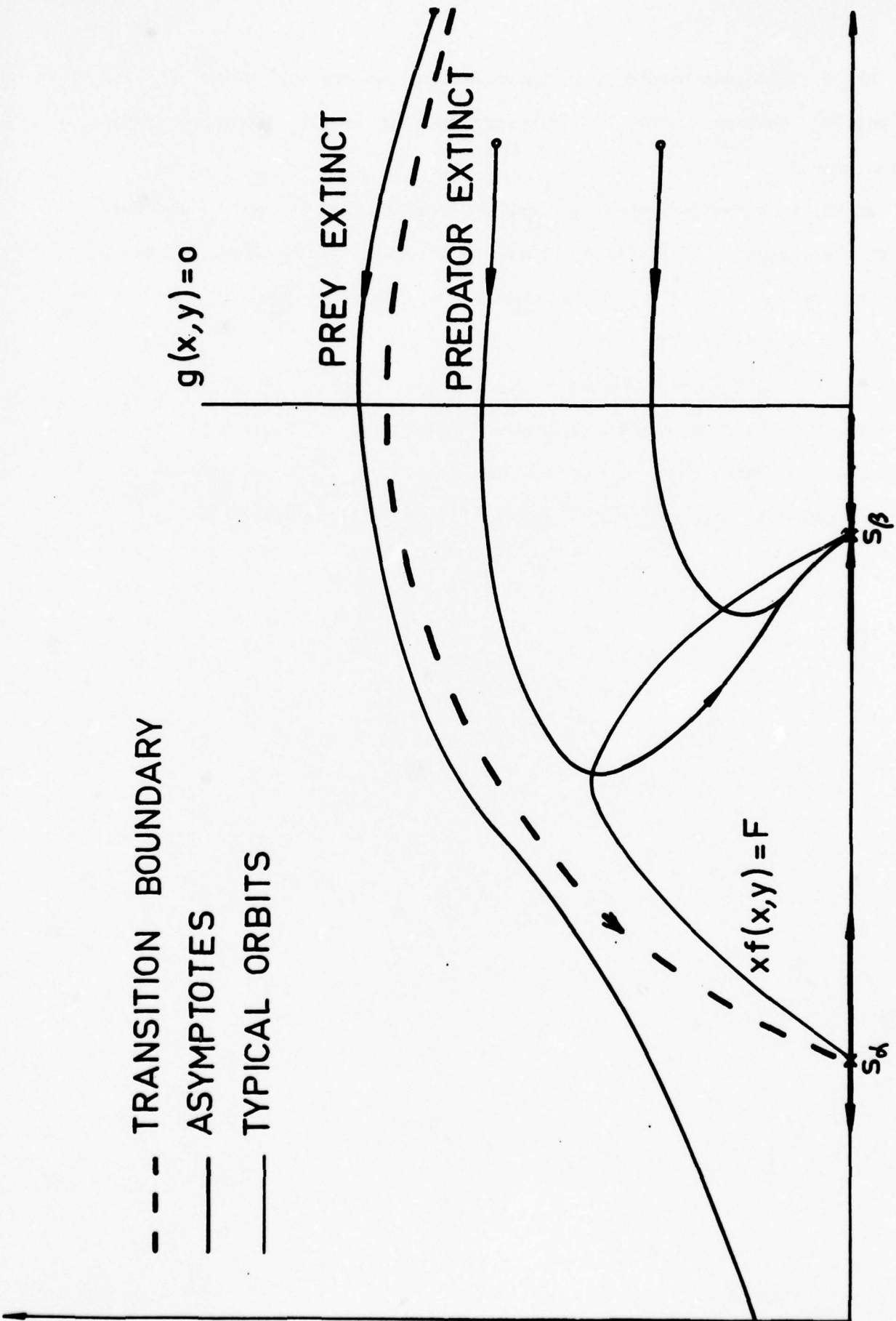
Just as in the predator-harvesting situation, we think of a homoclinic-type orbit (case 2) as a transitional case between cases 1 and 3. By solving the system (1) backwards in time numerically from an initial point near the saddle point S_α , we can distinguish between case 1 (for which this solution is unbounded as $t \rightarrow -\infty$) and case 3 (for which this solution tends to P_∞ or to a limit cycle around P_∞ as $t \rightarrow -\infty$). Thus we can approximate the value of F for which a transition occurs, and in addition we can approximate the region of asymptotic stability if the system is in case 1. If the system is in case 3b as $F \rightarrow F_C$, then the value F_C is meaningless biologically; the critical prey

harvest rate which produces prey extinction is the rate for which the system changes to case 3b, either from case 3a or from case 1b via case 2b. This rate can be determined only by numerical approximation.

The prey harvesting situation differs from the predator harvesting situation in that there are two possibilities for $F \geq F_C$. These are distinguished by the behavior for $F < F_C$ as F approaches F_C . If (5) is satisfied, then P_∞ and S_β coalesce as $F \rightarrow F_C^-$, and for $F < F_C$ sufficiently close to F_C there is a (full) orbit connecting P_∞ and S_β as t runs from $-\infty$ to $+\infty$. As this orbit is a separatrix at S_β , the system must be in case 1a as $F \rightarrow F_C^-$ and the orbit must run from S_β to P_∞ . The system is in case 1a at F_C if and only if the trace of $A[P_\infty(F_C)]$ is negative, or

$$(7) \quad Jf_x(J,0) + f(J,0) < 0.$$

If (7), or equivalently (5), is satisfied, then there are two equilibria $S_\alpha(\alpha,0)$ and $S_\beta(\beta,0)$ with $\alpha < \beta < J$ for $F > F_C$ it is easy to verify that S_α is a saddle point, while S_β is an asymptotically stable node. There is an asymptotically stable separatrix at the saddle point S_α ; solutions with initial value above this separatrix reach the y-axis in finite time (prey extinction), while solutions with initial value below the separatrix tend to the asymptotically stable equilibrium S_β as $t \rightarrow \infty$ (ultimate predator extinction). This is illustrated in Figure 6.



$F > F_c, P_\infty(F)$ asymptotically stable

Fig. 6

As F increases beyond F_C , there is a second critical value F^* for which S_α and S_β coalesce. For $F > F^*$, every solution of (1) reaches the y -axis in finite time.

If (6) is satisfied, then P_∞ and S_α coalesce as $F \rightarrow F_C^-$, and for $F < F_C$ sufficiently close to F_C there is an orbit running from P_∞ to S_α as t runs from $-\infty$ to $+\infty$. In this case the system (1) must be in case 3b as $F \rightarrow F_C^-$, or equivalently

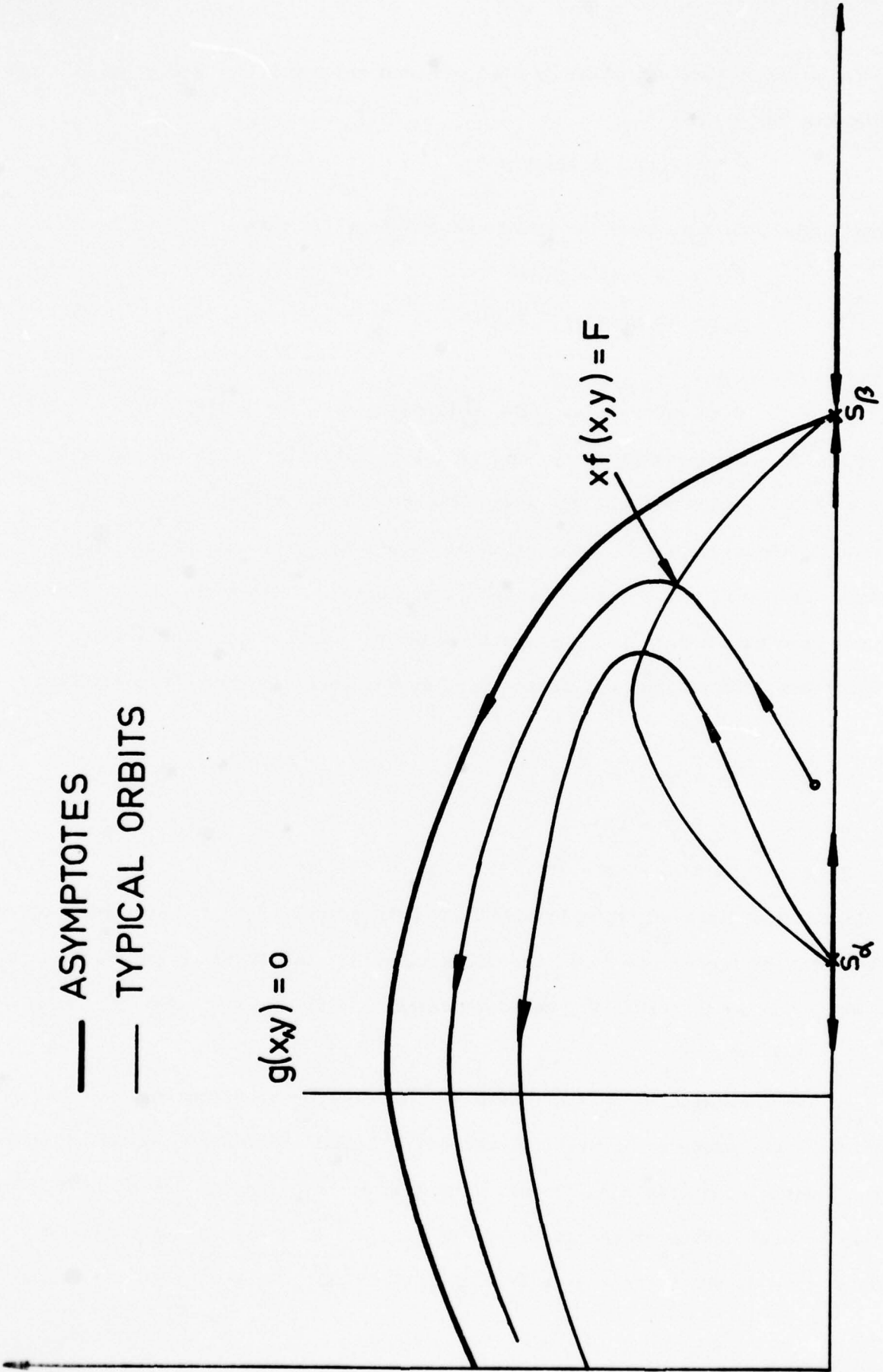
$$(8) \quad J f_x(J,0) + f(J,0) > 0.$$

For $F > F_C$ there are two equilibria $S_\alpha(\alpha,0)$ and $S_\beta(\beta,0)$, with $J < \alpha < \beta$. It is easy to verify that S_β is a saddle point, S_α is an unstable node, and every solution of (1) reaches the y -axis in finite time (Figure 7).

— ASYMPTOTES
 — TYPICAL ORBITS

$g(x,y) = 0$

$xf(x,y) = F$



$F > F_C, P_\infty(F_C)$ unstable

Fig.7

For a large class of commonly used predator-prey models, $g(x,y)$ is independent of y and

$$(9) \quad x f_{xy}(x,y) + f_y(x,y) < 0 .$$

In particular, this is true for models of the form (1) with

$$f(x,y) = \phi(x) - y\psi(x)$$

$$g(x,y) = s[x\psi(x) - J\psi(J)],$$

if

$$\psi(x) \geq 0, \psi'(x) \leq 0, \frac{d}{dx}[x\psi(x)] = x\psi'(x) + \psi(x) \geq 0 .$$

If $g(x,y)$ is independent of y and if (9) is satisfied, then the trace of the matrix $A(P_\infty)$ increases as P_∞ moves down the curve $g(x,y) = 0$. Thus as F increases, the real parts of the eigenvalues of $A[P_\infty(F)]$ can change from negative to positive but not in the other direction. Thus increasing the prey harvest rate can destabilize the equilibrium P_∞ but can not stabilize it. As F increases from 0 to F_C there are four possible case transitions, namely

- | | |
|-----|---|
| I | 1a |
| II | 1b \rightarrow 2b \rightarrow 3b |
| III | 1a \rightarrow 1b \rightarrow 2b \rightarrow 3b |
| IV | 1a \rightarrow 2a \rightarrow 3a \rightarrow 3b . |

In all but the first of these transitions there exists $F_H < F_C$ for which there is an orbit of homoclinic type. In transitions III and IV there exists $F_S < F_C$ for which the equilibrium P_∞ becomes unstable, with $F_S < F_H$ for III and $F_S > F_H$ for IV.

In the next section we shall examine the same class of models which we studied in the predator harvesting problem, and shall demonstrate which of the four possible transitions may occur. The transitions I and II can be identified easily by examination of the stability of P_∞ as F increases, although the harvest rate at which the change from case 1b to case 2b to case 3b occurs in II

can be found only by a computer simulation. Likewise, the distinction between III and IV, as well as the harvest rate at which transition occur, can be found only by a computer simulation.

3. A Class of Examples

The choice

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

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

has been used to model predator-prey interactions [Holling (1965)]. For this choice it is easy to calculate

$$x_{\infty}(F) = J, \quad y_{\infty}(F) = (J+A)[r(1 - \frac{J}{K}) - \frac{F}{J}]$$

and that the equilibrium $P_{\infty}(F)$ is asymptotically stable if and only if

$$F < \frac{rJ^2}{KA} (2J + A - K).$$

We define

$$(10) \quad F_S = \frac{rJ^2}{KA} (2J + A - K),$$

and then the equilibrium P_{∞} is asymptotically stable for $F < F_S$ and unstable for $F > F_S$. We determine F_C from $y_{\infty}(F_C) = 0$, which gives

$$(11) \quad F_C = \frac{rJ}{K} (K - J).$$

Using (10) and (11), it is easy to verify that if $K < 2J$, then $F_S > F_C$, and thus P_{∞} is asymptotically stable for $0 \leq F \leq F_C$ (transition I). If $K > 2J + A$, then $F_S < 0$, and thus P_{∞} is unstable for $0 \leq F \leq F_C$ (transition II). If $2J < K < 2J + A$, we have $0 < F_S < F_C$, which implies either transition III or transition IV.

The numbers α and β are the roots of

$$rx(1 - \frac{x}{K}) - F = 0,$$

namely

$$\alpha = \frac{K}{2} - \left\{ \left(\frac{K}{2} \right)^2 - \frac{KF}{r} \right\}^{1/2}, \quad \beta = \frac{K}{2} + \left\{ \left(\frac{K}{2} \right)^2 - \frac{KF}{r} \right\}^{1/2}.$$

If $K < 2J$, then $\alpha(F_C) = K - J < J$, $\beta(F_C) = J$, while if $K > 2J$, $\alpha(F_C) = J$, $\beta(F_C) = K - J > J$. In the case $K < 2J$ in which $P_\infty(F_C)$ is asymptotically stable,

the value F^* for which P_α and P_β coalesce is given by

$$rK^2 - 4KF^* = 0,$$

or

$$(12) \quad F^* = \frac{rK}{4}.$$

We now give examples to illustrate the possibilities.

Example I: $r = 1, s = 1, K = 40, A = 10, J = 30$. Since $K < 2J$, the system is in case 1a for $0 \leq F \leq F_C = 7.5$, and $F^* = 10.0$. The simulations for $F = 2, F = 4, F = 7.5$, and $F = 9$ (Figures 8-11) indicate that the region of asymptotic stability shrinks as F increases. For $F < 7.5$, the separatrix at S_α divides the region of coexistence from the region of prey extinction. For $7.5 < F < 10.0$, we have a new phenomenon, which cannot occur for predator harvesting but which is predicted by the theory, namely that the separatrix at S_α now divides the first quadrant of the x - y plane into a region of prey extinction and a region of predator extinction. Note the expanded scales in Figures 10 and 11.

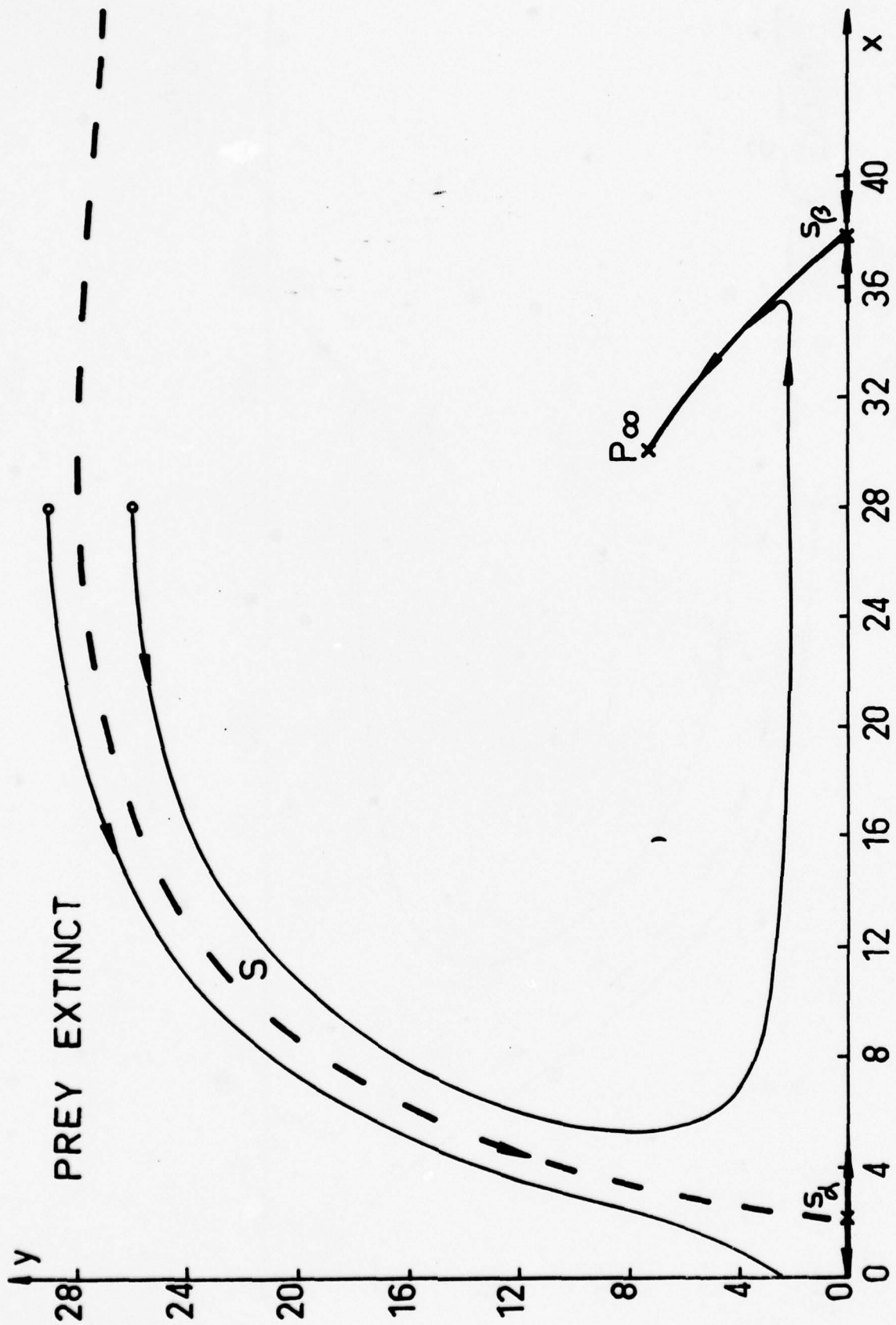


Fig.8

Example 1. $F=2$. Case 1a.

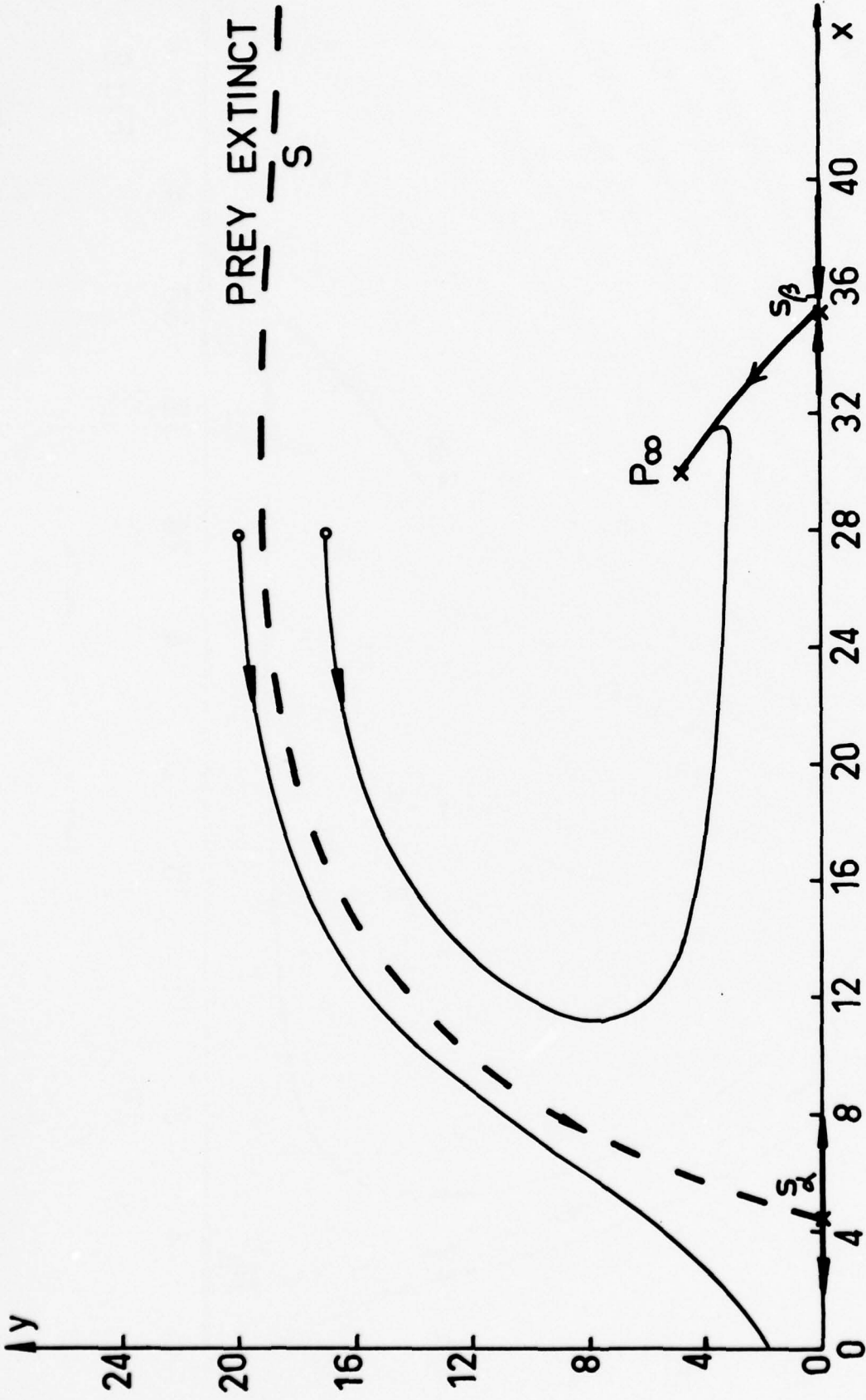


Fig.9

Example 1. $F=4$. Case 1a.

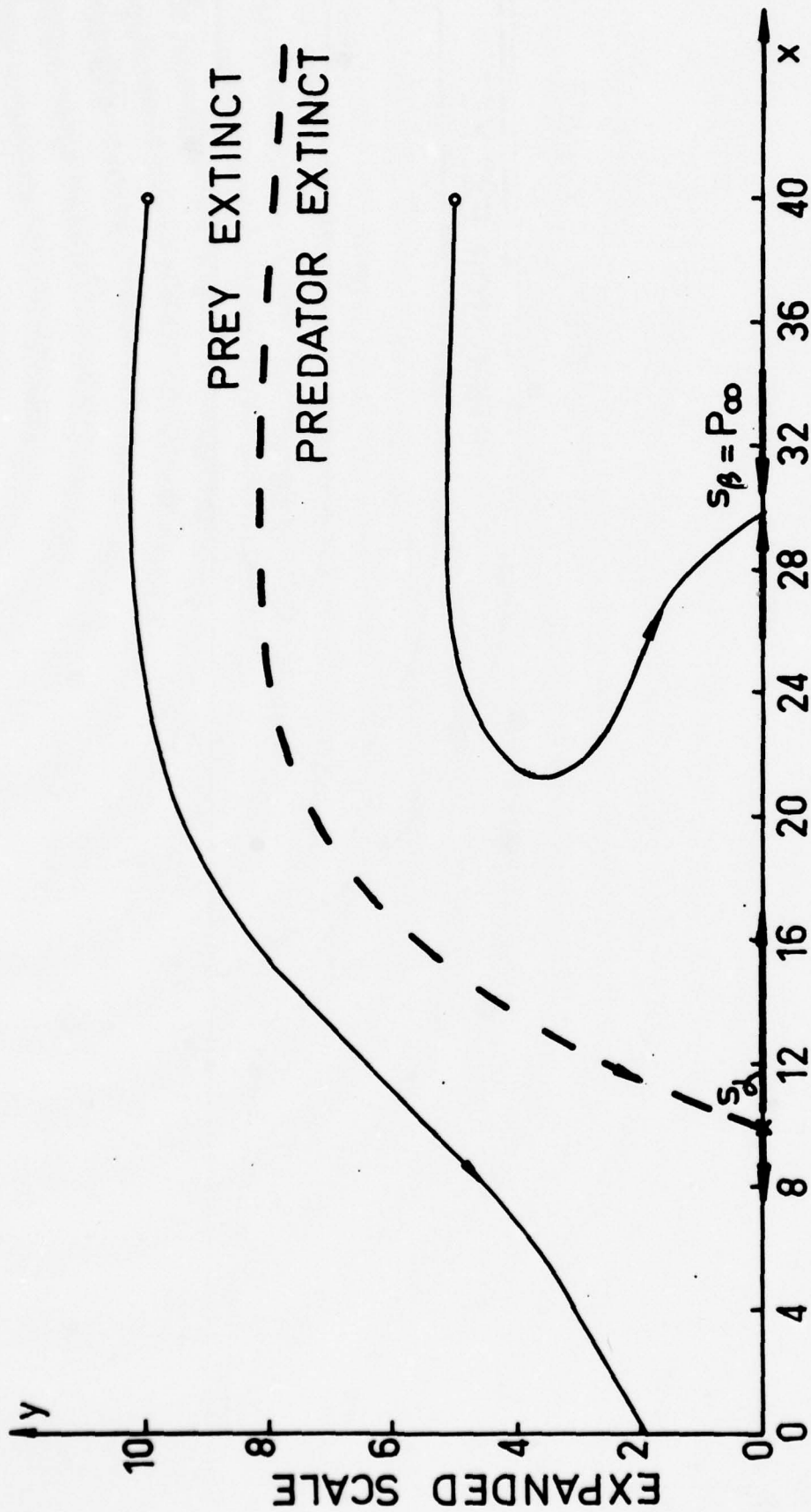


Fig.10

Example 1. $F=F_C=7.5$. Case 1a.

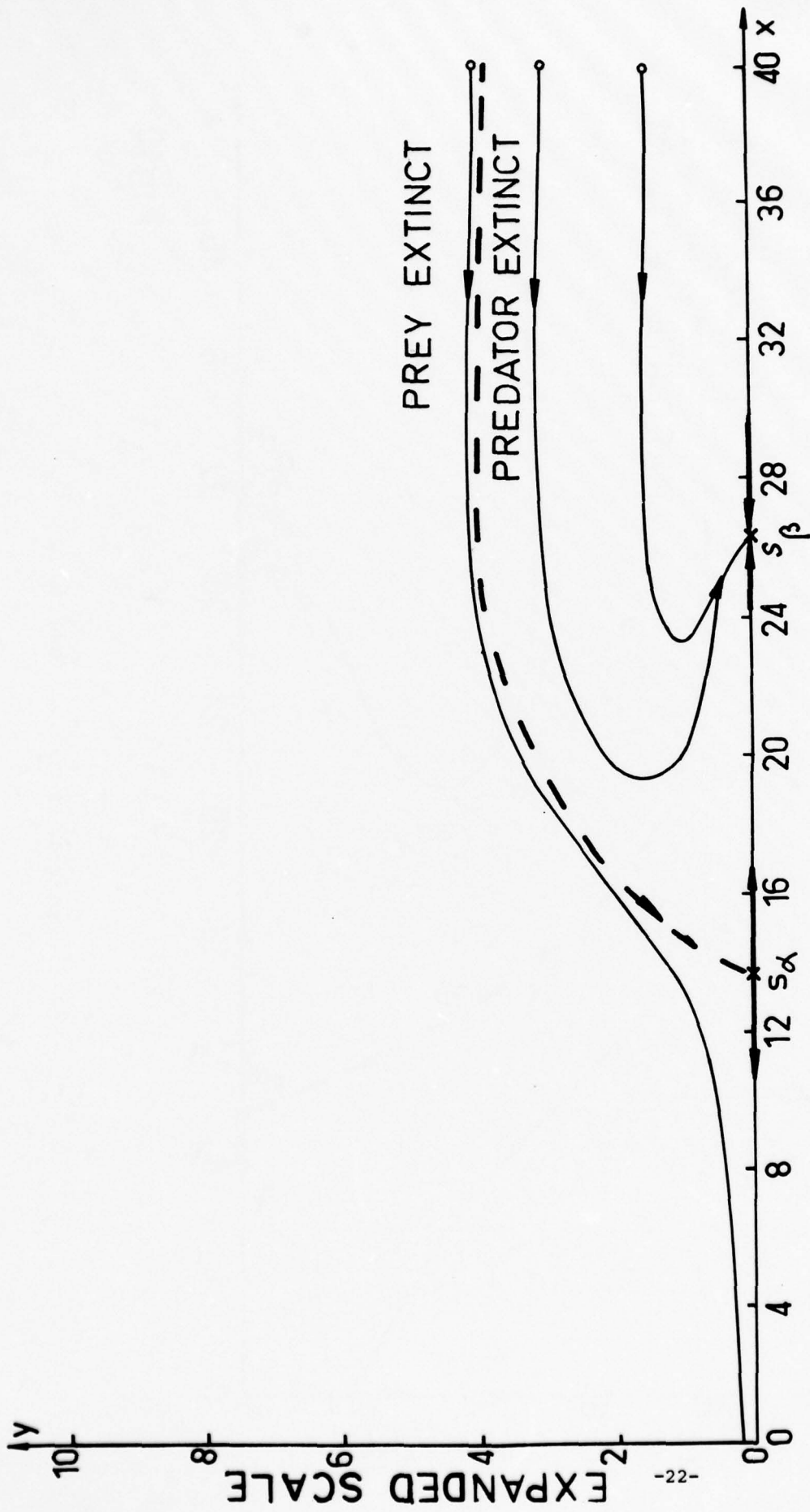


Fig. 11

Example 1. $F=9 > F_C$.

Example II: $r = 1, s = 1, K = 40, A = 10, J = 10$. Since $K > 2J + A$, the equilibrium P_∞ is unstable for $0 \leq F \leq F_C = 7.5$. Thus there exists $F_H < F_C$ for which there is a homoclinic-type orbit and a transition from case 1b to case 2b to case 3b. A computer simulation (Figures 12-15) shows that $F_H \approx 0.357$, and that the region of asymptotic stability shrinks as F increases. The system collapses for $F = F_H$, although a local stability analysis might suggest that harvest rates up to F_C are safe. Even for harvest rates less than F_H , the limit cycle comes so close to the x-axis that a small perturbation could produce predator extinction and collapse of the system. Note the expanded scale in Figure 15.

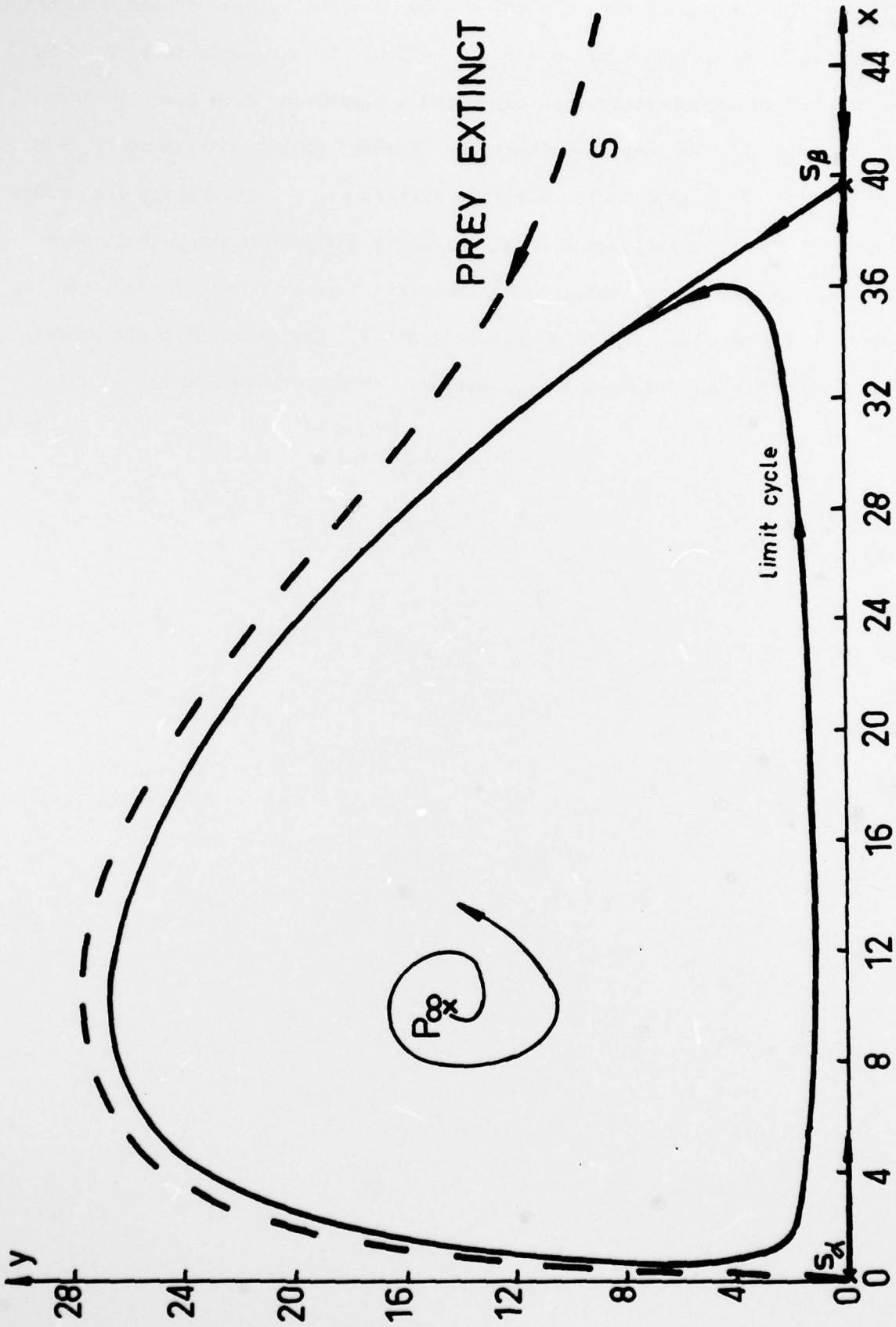


Fig.12

Example 2. $F=0.3$. Case 1b.

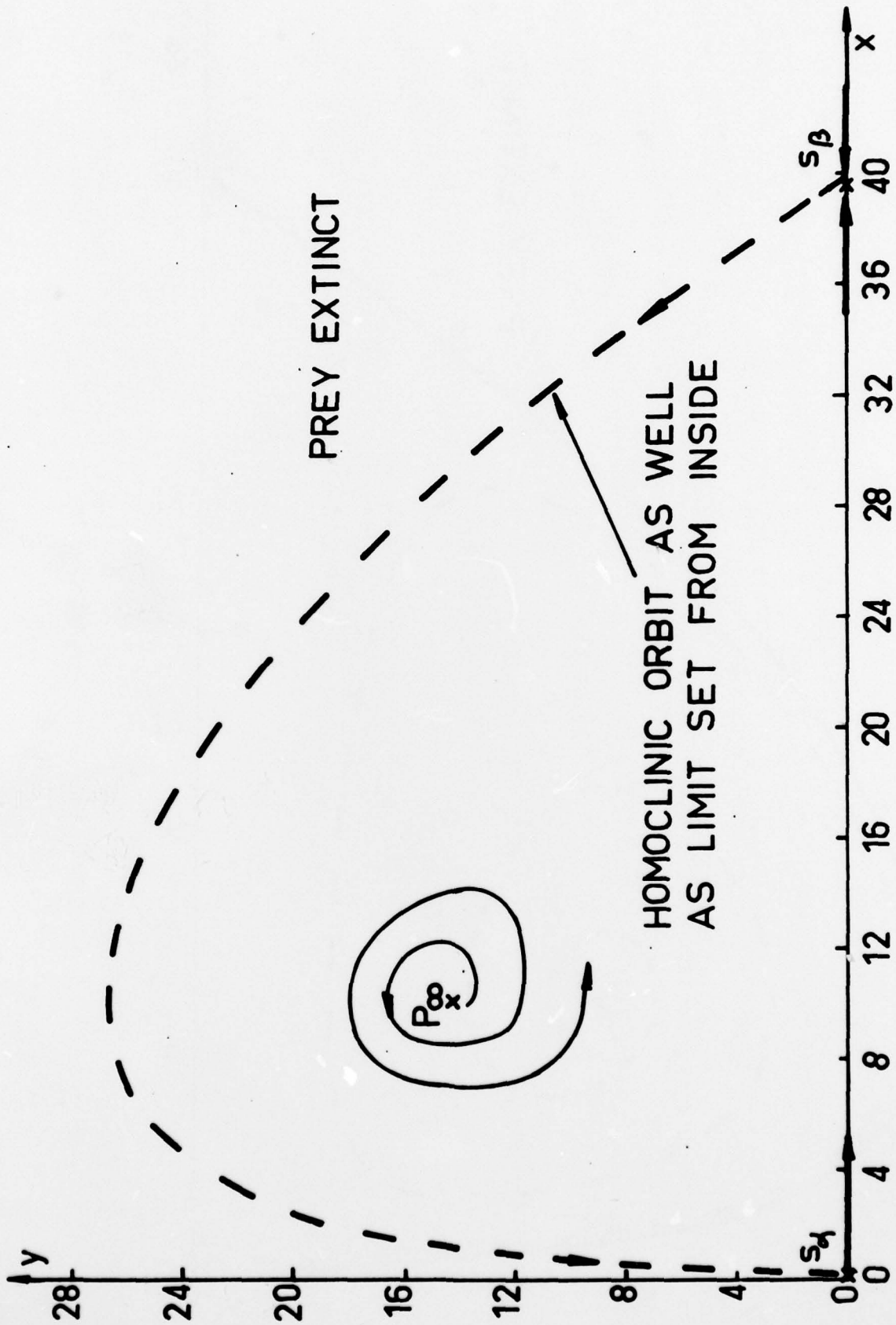


Fig.13

Example 2. $F=0.357$. Case 2b.

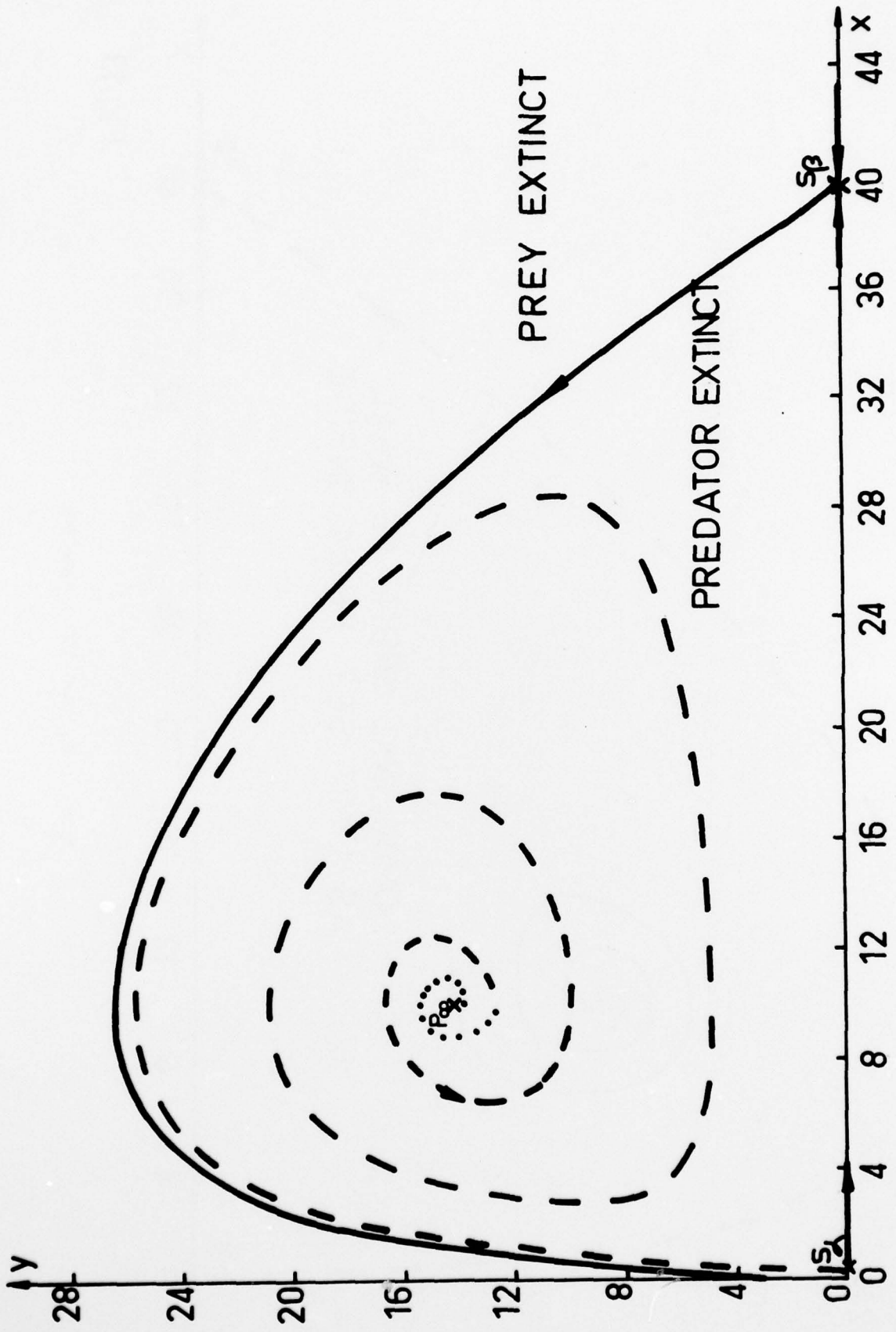


Fig.14

Example 2. $F=0.4$. Case 3b.

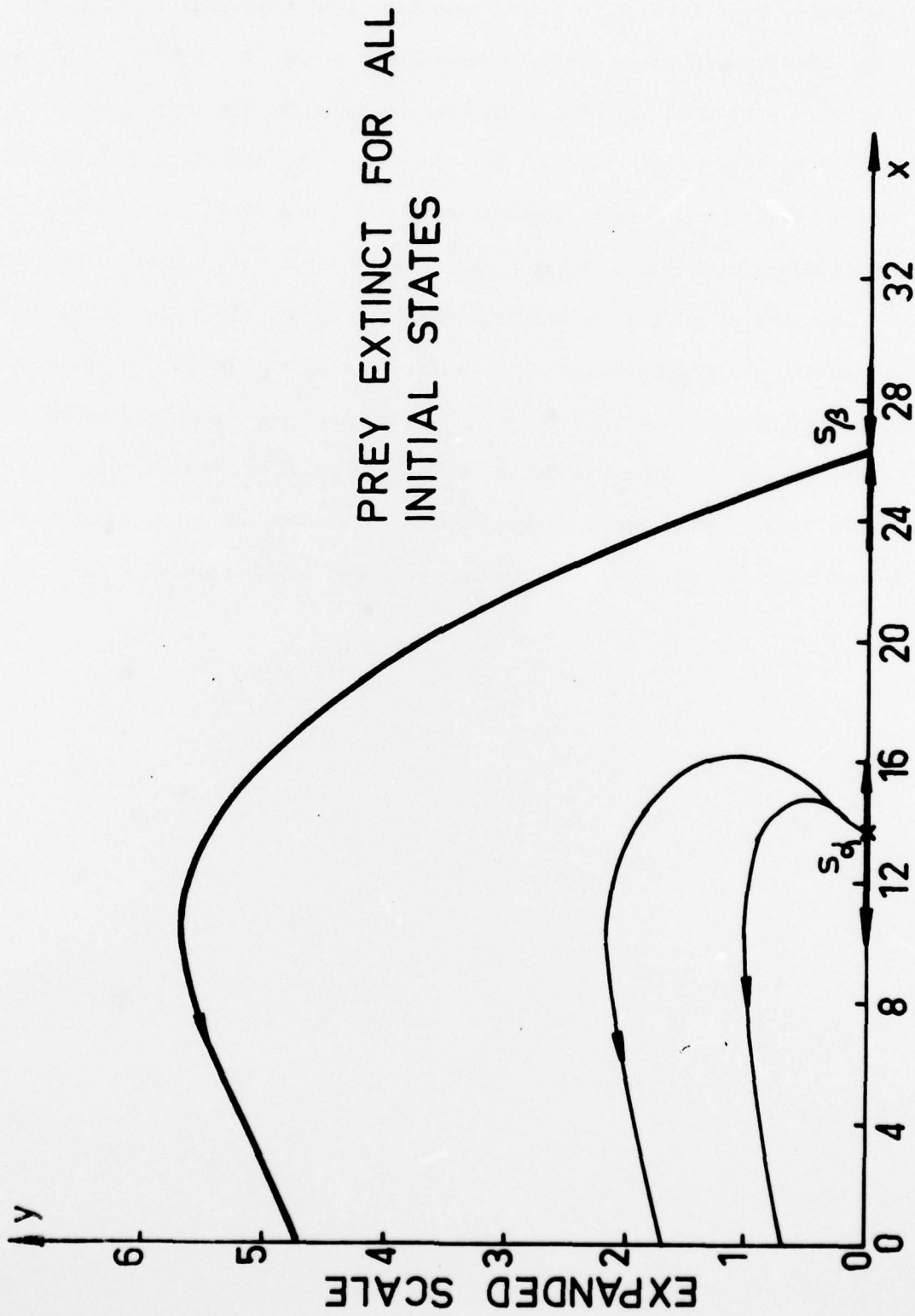


Fig. 15

Example 2. $F=9 > F_C$.

Example III: $r = 1, s = 1, K = 40, A = 10, J = 19$. Since $2J < K < 2J + A$, there exists $F_S < F_C$ for which the equilibrium P_∞ becomes unstable; from (10) and (11) we find $F_S = 7.22, F_C = 9.975$. We know also that there must exist $F_H < F_C$ for which there is an orbit of homoclinic type. If $F_S < F_H$, the transition is $1a \rightarrow 1b \rightarrow 2b \rightarrow 3b$ and the effective collapse of the system is at F_H , while if $F_S > F_H$, the transition is $1a \rightarrow 2a \rightarrow 3a \rightarrow 3b$, and the effective collapse of the system is at F_S . Only a computer simulation can distinguish between these possibilities, and this indicates that $F_H \approx 7.815 > F_S$, showing that the transition is $1a \rightarrow 1b \rightarrow 2b \rightarrow 3b$ (Figures 16-20). Again, the region of asymptotic stability shrinks as F increases. Even for $F = 7$, the region of asymptotic stability has a narrow "neck" for large x , and small perturbations could drive the system to collapse. In a practical sense, the maximum safe harvest rate - for which the region of asymptotic stability is of reasonable size and for which orbits do not come too close to the x -axis - is still smaller than F_H .

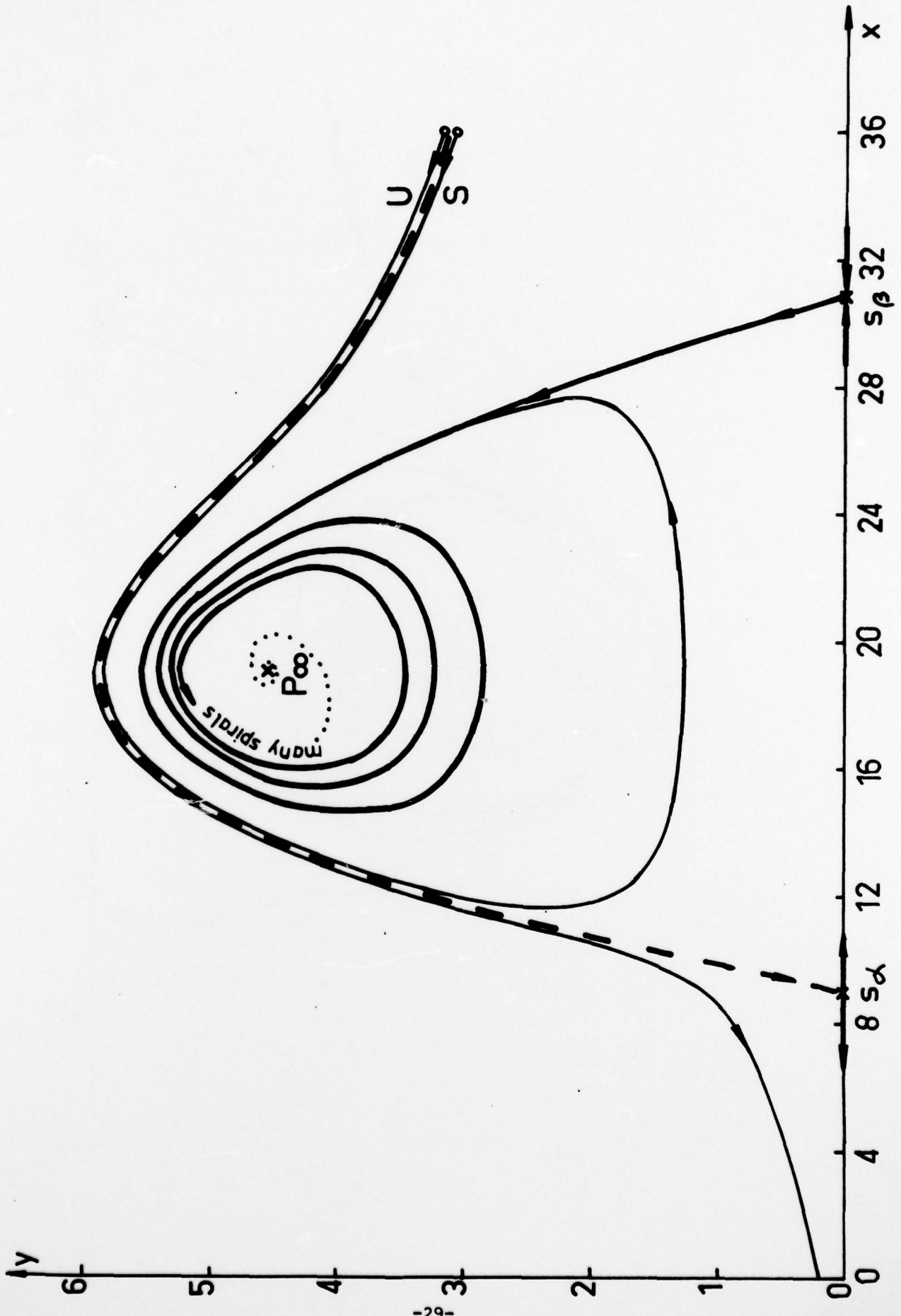


Fig. 16

Example 3. $F=7$. Case 1a.

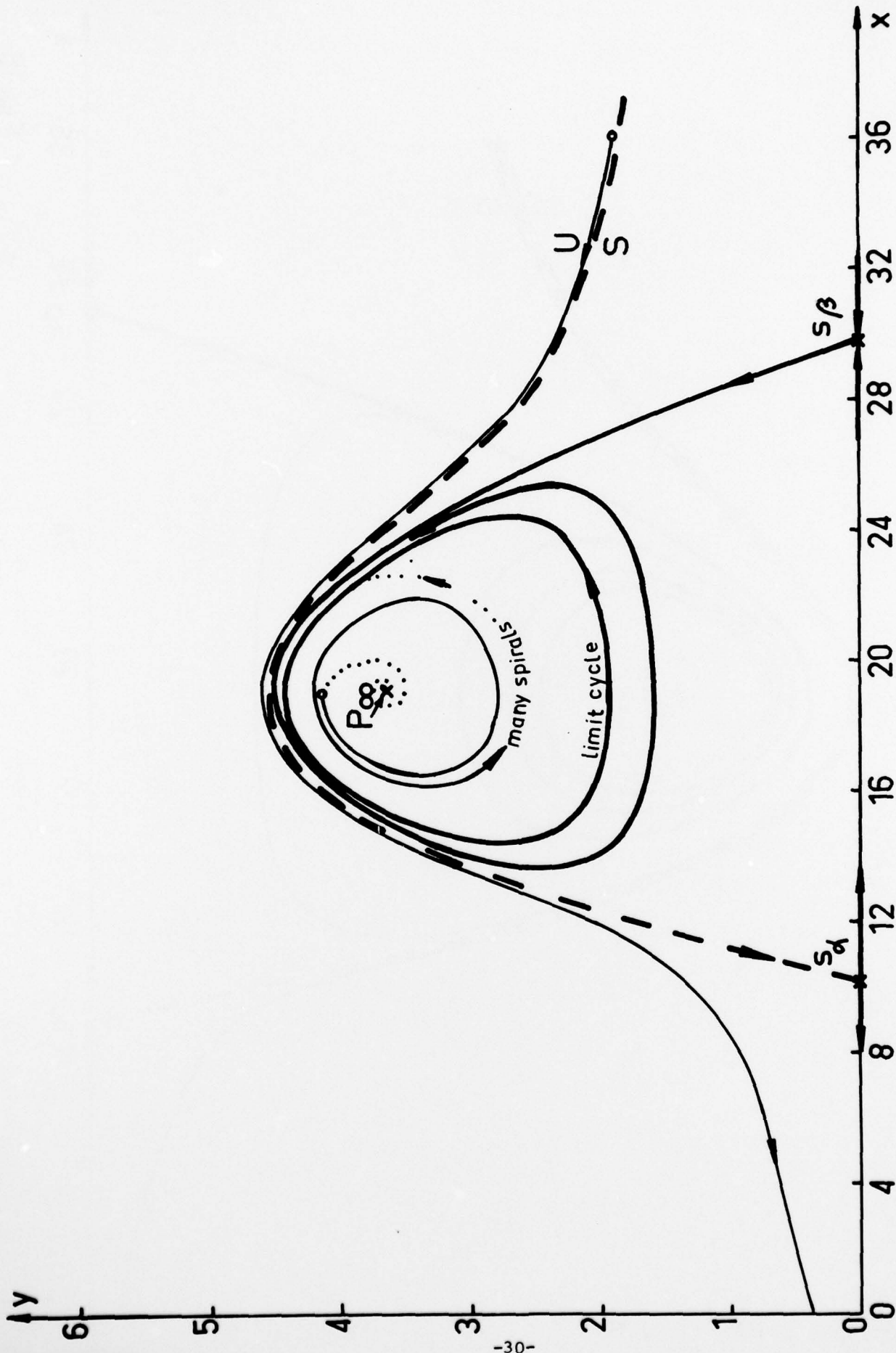


Fig.17

Example 3. $F=7.6$. Case 1b

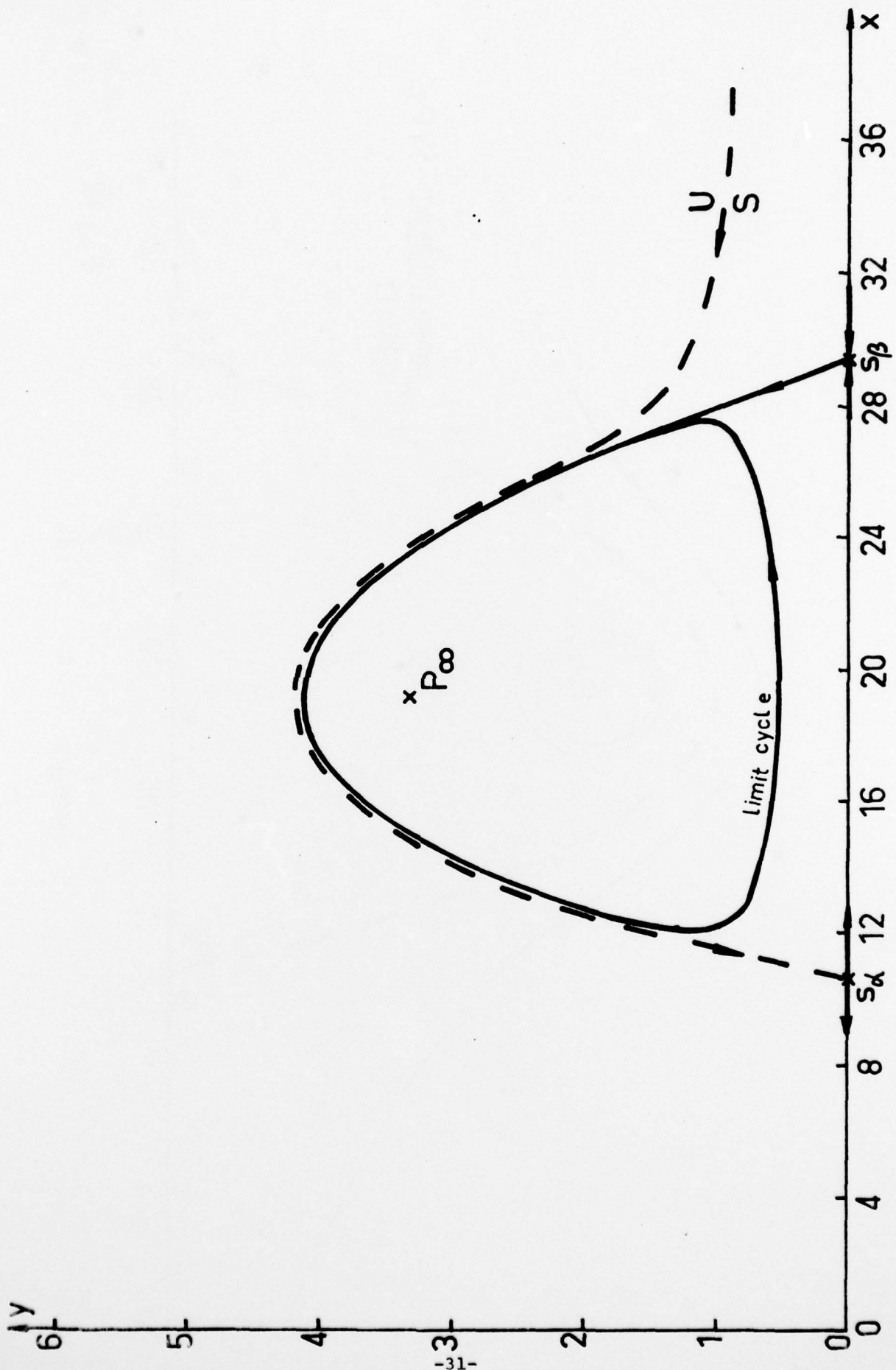


Fig.18

Example 3. $F=7.8$. Case 1b.

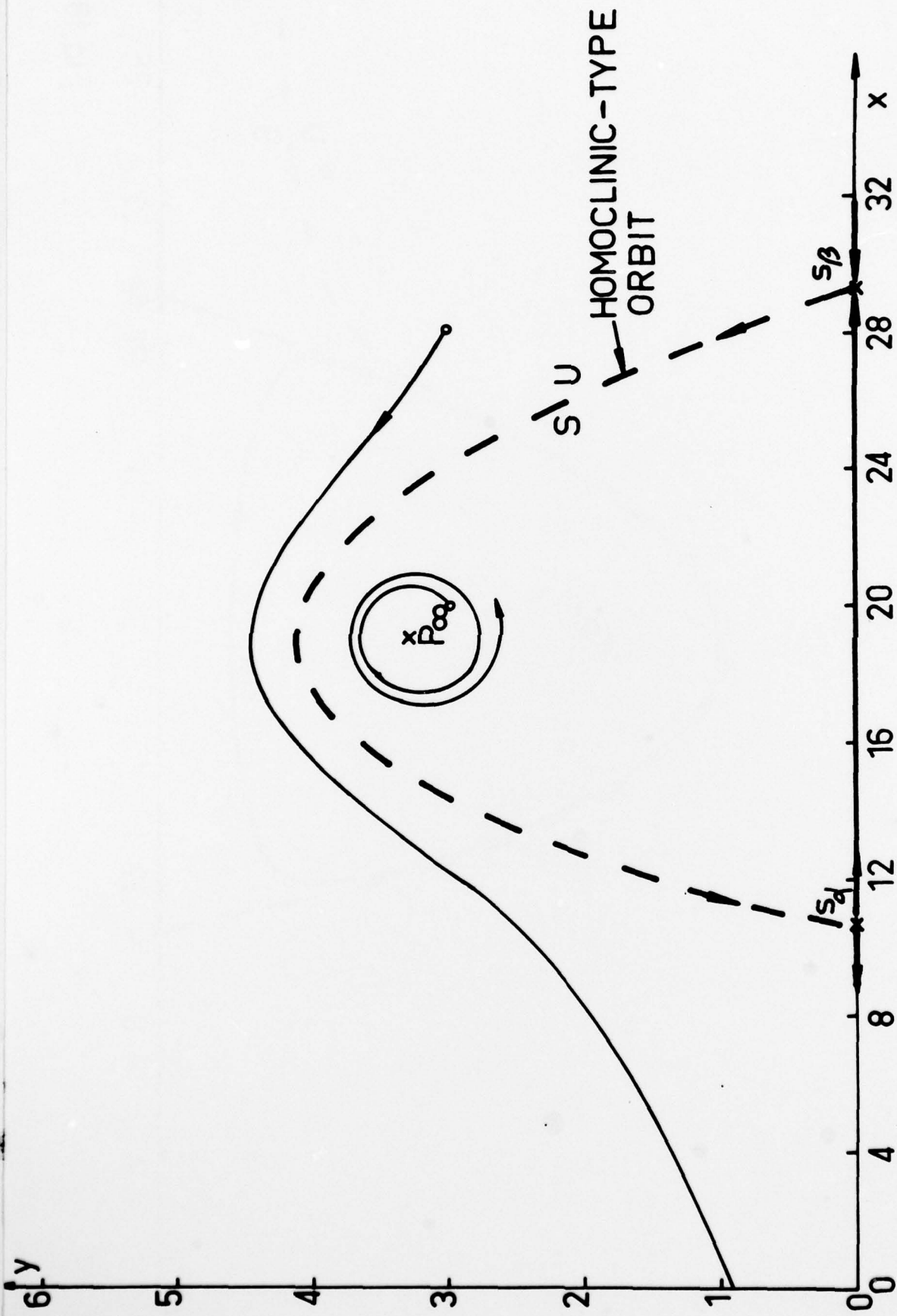


Fig.19

Example 3. F=7.815. Case 2b

We have been unable to construct an example of the transition $1a \rightarrow 2a \rightarrow 3a \rightarrow 3b$. Some attempts with J very close to $K/2$ appeared to be of this type, but closer examination disclosed that they were actually $1a \rightarrow 1b \rightarrow 2b \rightarrow 3b$. We conjecture that examples of the desired type exist but are very fragile, both in the biological sense that the system survives only for a very small set of initial conditions and in the mathematical sense that F_H is very close to F_S so that the system is in case 3a for only a small range of harvest rates.

4. Conclusions

We are studying a class of systems with two saddle points on the x -axis and an equilibrium in the interior of the first quadrant. By locating the separatrices at the saddle points, which requires a computer simulation and by studying the local stability of the equilibrium, we can describe completely the global structure of solutions. Our examples indicate that, just as for predator-harvesting, the system may collapse for harvest rates much smaller than would be considered safe on the basis of a purely local stability analysis. In particular, if the equilibrium is unstable at the maximum harvest rate F_C suggested by a local analysis, then the system must already have collapsed.

A new phenomenon, which cannot occur under predator harvesting, occurs for harvest rates greater than F_C if the equilibrium is stable at F_C . In this case there is a range of harvest rates for which there is a separatrix dividing the first quadrant into a region of prey extinction and predator survival (although prey extinction will ultimately lead to predator extinction as well) and a region of prey survival and predator extinction. For still larger harvest rates, the prey species becomes extinct for all initial values, as one would expect. Compared to the predator harvesting problem, there is a simpler structure with fewer possibilities.

We propose to investigate the simultaneous harvesting of both species. Since there are theoretical differences between systems with both species harvested and systems with no predator harvesting, we shall study only systems in which there is some predator harvesting. The study of systems without predator harvesting has been carried out here.

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