ANALYSIS OF A COMPACT PREDATOR-PREY MODEL
I. THE BASIC EQUATIONS AND BEHAVIOUR

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Introduction

This paper is the first of a series dealing with the analysis of a compact, relatively uncomplicated predator-prey model. Here, only the basic equations are given and a selected subset of system behaviour illustrated. Written documentation concerning this model and its analytic investigation are being documented as completed to speed communication among interested parties. As this model is becoming a focus for several methodological and conceptual discussions, the need has arisen for a concise description of the equations.

The model itself stands midway between more traditional differential or difference equation systems and complex simulation models. (For a review of systems of the former type and access to the flavor of their behaviour, see May, 1973 or Maynard Smith, 1974.) This model is not an embellishment of simpler classic equations but rather an aggregation and consolidation of a complex detailed predator-prey simulation model developed from an extensive program of experiment and submodel development (Holling, 1965, 1966a, Griffiths and Holling, 1969). The objectives of that program are best summarized in Holling 1966b. The complete model continues to be refined, but a detailed documentation, with primary emphasis on the predation process has been prepared (Holling, 1973b). In its present form the model is a synthesis of the best validated components of the analog processes of predation and parasitism.

The performance of the simulation model exhibits dynamic systems behaviour with far-reaching conceptual and theoretical implications. Holling's paper (1973a) on the resilience of ecological systems is the overture to a major reorientation of ecological perspective. To further explore the dynamic properties of this class of system, we mathematically and pragmatically require an analytic system that is tractable while providing the rich variety of behaviour found in the full simulator.

The goal of this series of IIASA working papers is to explore the dynamic topology of this analytic system and outline a general protocol for analysis of similar systems. There is clearly room to venture back into the ecological domain and use this model to gain insight into the biological aspects of the predation process. However, such a move is not envisioned in the current context. In a subsequent paper I will include a discussion of the theoretical and experimental foundations of this model complete with ecological assumptions and limitations. At present I am offering a system of equations for mathematical enquiry.

The Model Equations

The model is equivalent to a deterministic pair of difference equations. Indeed it can be so formulated, but to do that would cloud, rather than clarify. The iteration time interval is unspecified in absolute terms. During each time step, predators attack and remove prey. Then predators and prey both reproduce. The event orientation of the formulation tie the iteration most strongly to the prey generation time.

The two state variables are the densities of predators and of prey. At the start of each iteration the initial densities are

$$\begin{aligned} x &= \text{initial prey density} \\ y &= \text{initial predator density} \end{aligned} \tag{1}$$

The functional response of predator attacks to prey density is

$$g(x) = \frac{a_1 x e^{\alpha x}}{1 + a_2 x e^{\alpha x}} = \frac{a_1 x}{e^{-\alpha x} + a_2 x} \quad . \tag{2}$$

Because attacks of predators on prey are distributed nonrandomly among the prey, we incorporate the negative binomial distribution to account for this (see Griffiths and Holling, 1969). The number (per unit area) of prey attacked is z and is expressed as

$$z = f(x,y) = x\left\{1 - \left[1 + \frac{k_1 \cdot y \cdot g(x)}{kx}\right]^{-k}\right\} \tag{3}$$

The number of prey that escape predation is

$$\hat{x} = x - z \quad . \tag{4}$$

These reproduce according to some function $H(\hat{x})$ that provides a density of prey x' at the beginning of the next time step. The reproduction function used is a descriptive one. It incorporates a minimum density reproduction threshold and a maximum at some finite prey density.

Prey reproduction depends on three parameters:

$$\begin{aligned} x_o &= \text{minimum density for reproduction} \\ M &= \text{maximum reproductive rate} \\ OPTX &= \text{prey density at maximum reproductive rate} \end{aligned} \tag{5}$$

These parameters are recombined as

$$\begin{aligned} \gamma &= 1 + OPTX \\ \mu &= OPTX - x_o = \gamma - 1 - x_o \\ CH &= \frac{M \cdot e^{\mu}}{\mu^{\mu}} = M\left(\frac{e}{\mu}\right)^{\mu} = M \cdot C_{\mu} \end{aligned} \tag{6}$$

The final form of $H(\hat{x})$ is

$$x' = H(\hat{x}) = CH \cdot e^{-(\hat{x}-x_o)} \cdot (\hat{x} - x_o)^{\mu} \cdot \hat{x} \quad . \tag{7}$$

The function describing predator reproduction incorporates both "contest" and "scramble" types (Nicholson, 1954). The parameter C, varyies between 0 and 1, and specifies the degree of scramble in the process. The predator density that begins the next iteration, y', is given as

$$y' = p(x,z) = c_1 \cdot z\left(1 - C \cdot z \frac{1 + k}{k \cdot x + z}\right) \quad . \tag{8}$$

In summary the equations are

$$g(x) = \frac{a_1 x}{e^{-\alpha x} + a_2 x} \tag{2}$$

$$z = f(x,y) = x\left\{1 - \left[1 + \frac{k_1 \cdot y \cdot g(x)}{kx}\right]^{-k}\right\} \tag{3}$$

$$\hat{x} = x - z \tag{4}$$

$$x' = H(\hat{x}) = CH \cdot e^{-(\hat{x}-x_o)} \cdot (\hat{x} - x_o)^{\mu} \cdot \hat{x} \tag{7}$$

$$y' = p(x,z) = c_1 z\left(1 - C \cdot z \frac{1 + k}{k \cdot x + z}\right) \tag{8}$$

The "graph" of this model is relatively simple (Figure 1). The quantity y' is entered twice to emphasize the symmetry. The broken arrows from x' to x and from y' to y indicate a new iteration in the time sequence.

Model Behaviour

A BASIC program was written to implement this model on a Hewlett-Packard 9830A calculator. A small subset of the possible conditions are illustrated in Figures 2 through 5.

In the course of development of this experimental and modelling work, certain parameters have evolved into what we call our "Standard Case". These particular values do not necessarily carry any fundamental biological significance; they only serve as a common base for comparing the effect of changes in parameter values. The "Standard Case" in the present notation is

$a_1 = 2.5$

$a_2 = 0.0714$

$\alpha = 0$

$k_1 = 30$

$k = 0.78$

$x_o = 0.001$

$\gamma = 1.1$

$M = 3.0$

$C = 0$

$c_1 = 0.95$

Figure 2 shows a phase plane trajectory for the Standard Case. The initial starting point is at "x"; the trajectory then spirals counter-clockwise into an equilibrium point. (The trajectory has been terminated before it reached that point.)

The Standard Case is not globally stable. Combinations of state variables that lead to prey densities less than x_o result in extinction of the prey population followed by the predators. Figure 3 shows an enlarged section of the state plane with a disperse collection of starting conditions. The actual trajectories have been surpressed in this plot. Initial points are marked with "x"; subsequent locations are marked with "O" if they are outside the domain of attraction or with "+" if they eventually lead to equilibrium. With enough trial initial points , the boundary of the attractor domain begins to be defined as indicated by the freehand curve.

Previous explorations with the full simulation model have identified k and C as important and sensitive parameters to the topology of trajectories (Jones, 1973). Figure 4 (a through f) illustrates a range of k values when C = 0 (i.e. "contest" predator reproduction Figure 5 (a through f) is for another k series when C = 1 ("scramble" reproduction).

The qualitative behaviour of figures 4 and 5 are summarized in Table I. The exact division between these modes have not been located. They could be, of course, given enough paper and patience. The goal of the present analytic effort is to shortcut that necessity and develop a more comprehensive procedure for looking at this type of system.

References

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Table I. Behaviour trend with increasing k, for C = 0 and C = 1.

k	C = 0	C = 1	k
0			0
	Long Narrow Domain of Attraction (perhaps extending to y = ∞)		
$\sim$ 0.4		Large Domain of Attraction (perhaps infinite in high x, y corner)	
0.6	Beginning of Oscillatory Trajectories. Finite Domain.		
0.825	Neutral Orbits Inside a Finite Domain		
			?
	Global Instability Increasing speed to extinction.		
		Finite Domain of Attraction Contraction of Domain	10
			100

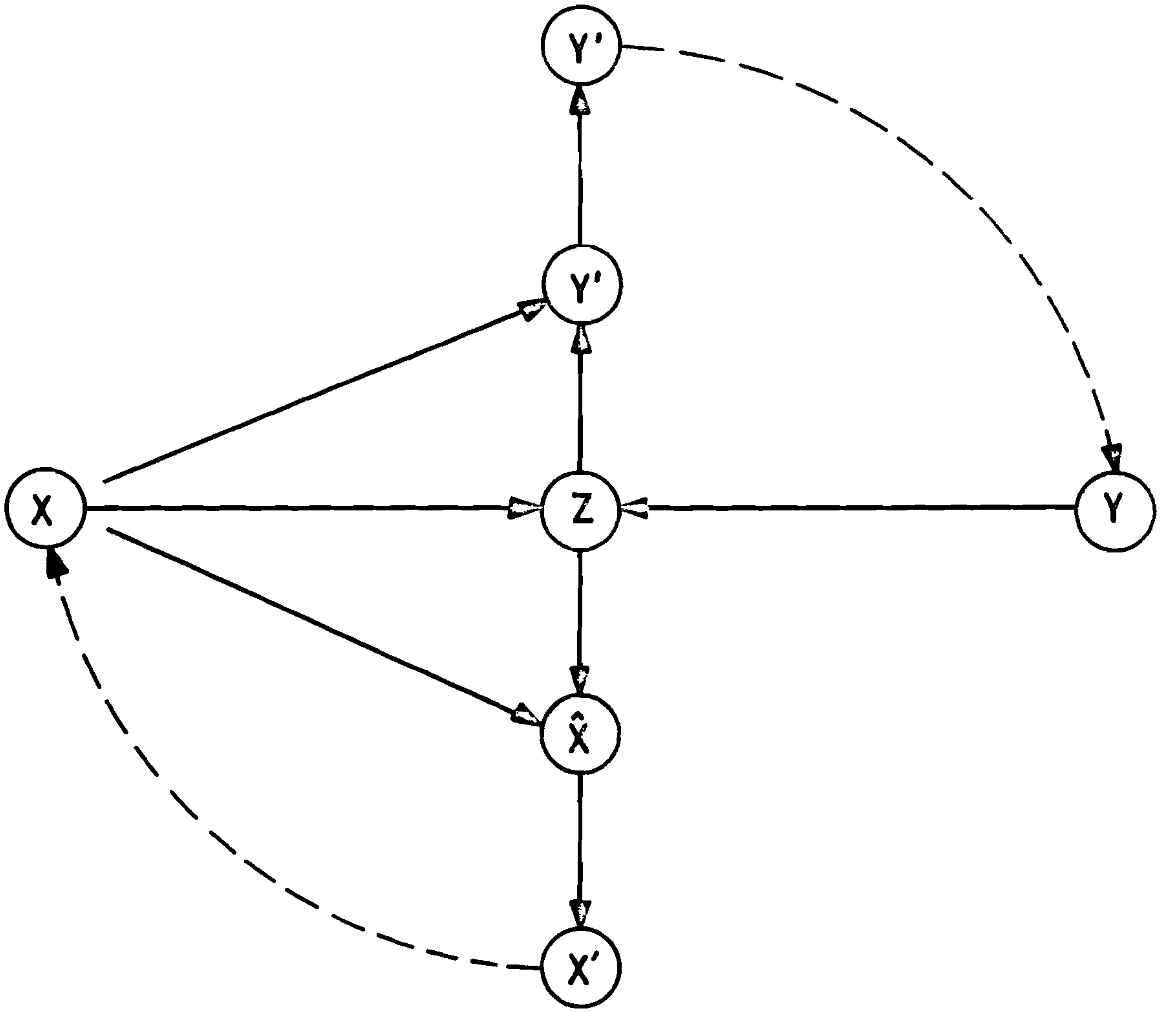

FIGURE 1: GRAPH OF COMPACT PREDATOR-PREY MODEL

Figure 2. Sample Trajectories for "Standard Case"

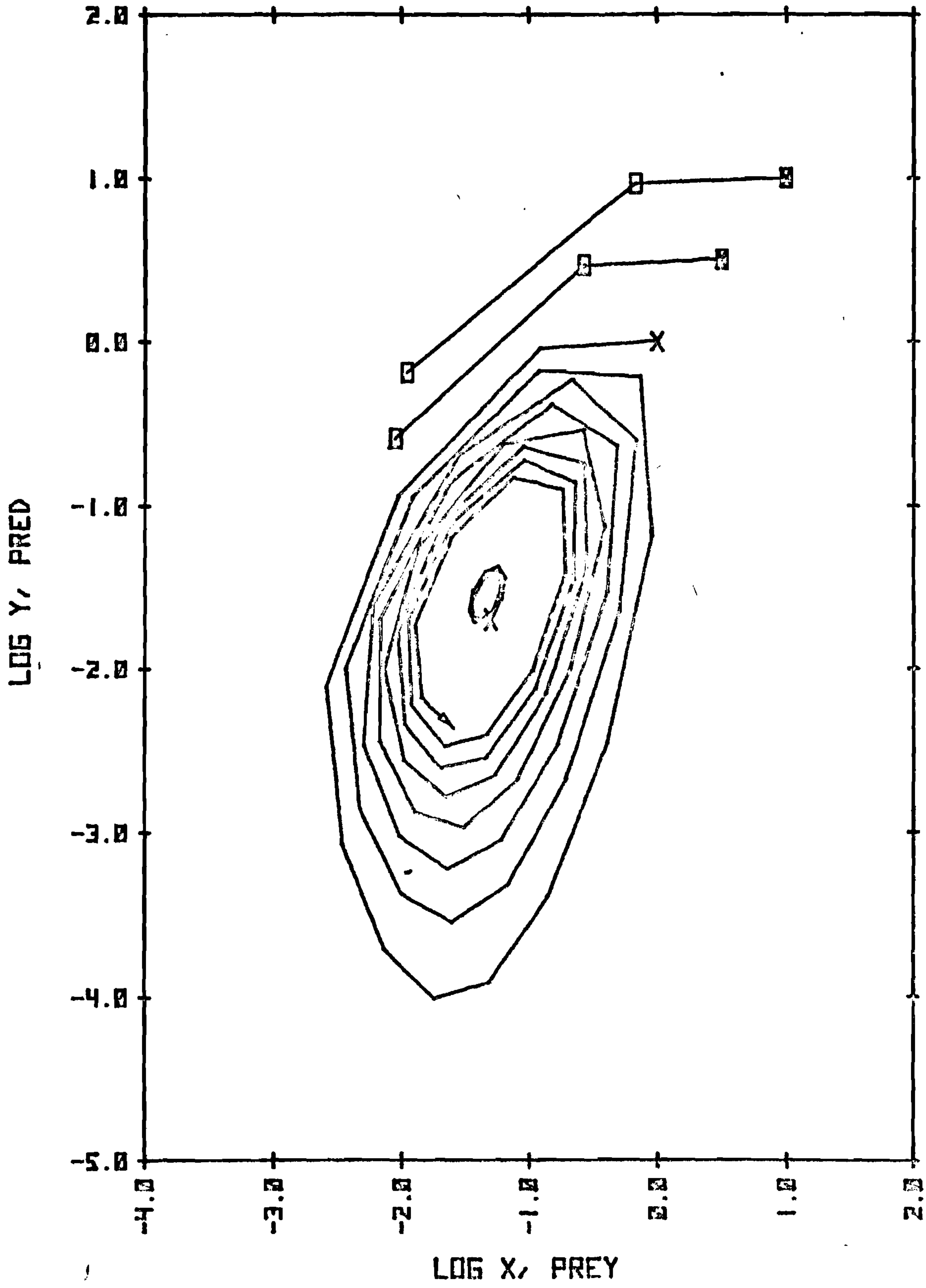

Figure 3. Domain of Attraction for "Standard Case"

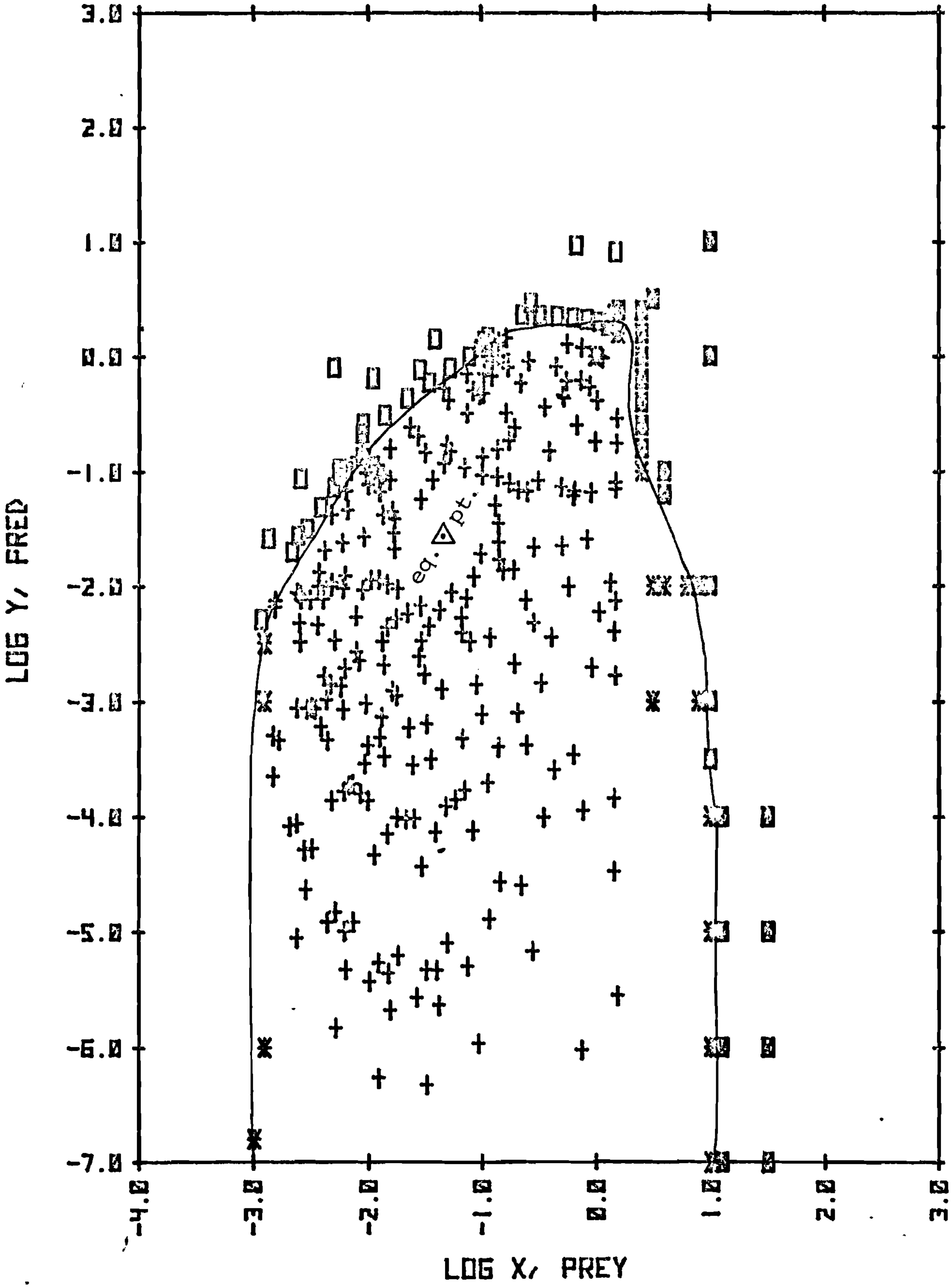

Figure 4a. Sample Phase Plane Trajectory for C = 0 and k = 0.05

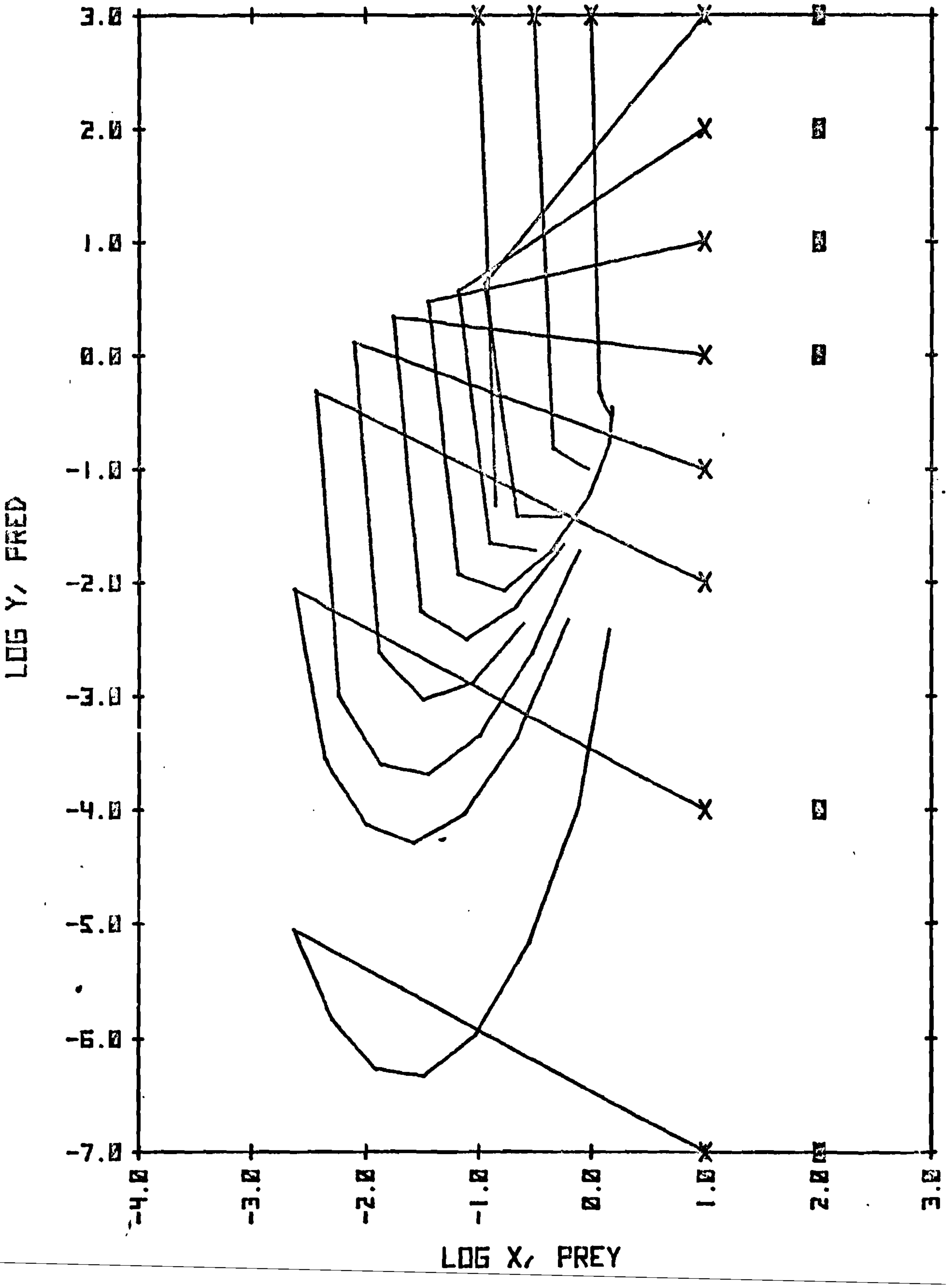

Figure 4b. Sample Phase Plane Trajectory for C = 0 and k = 0.2

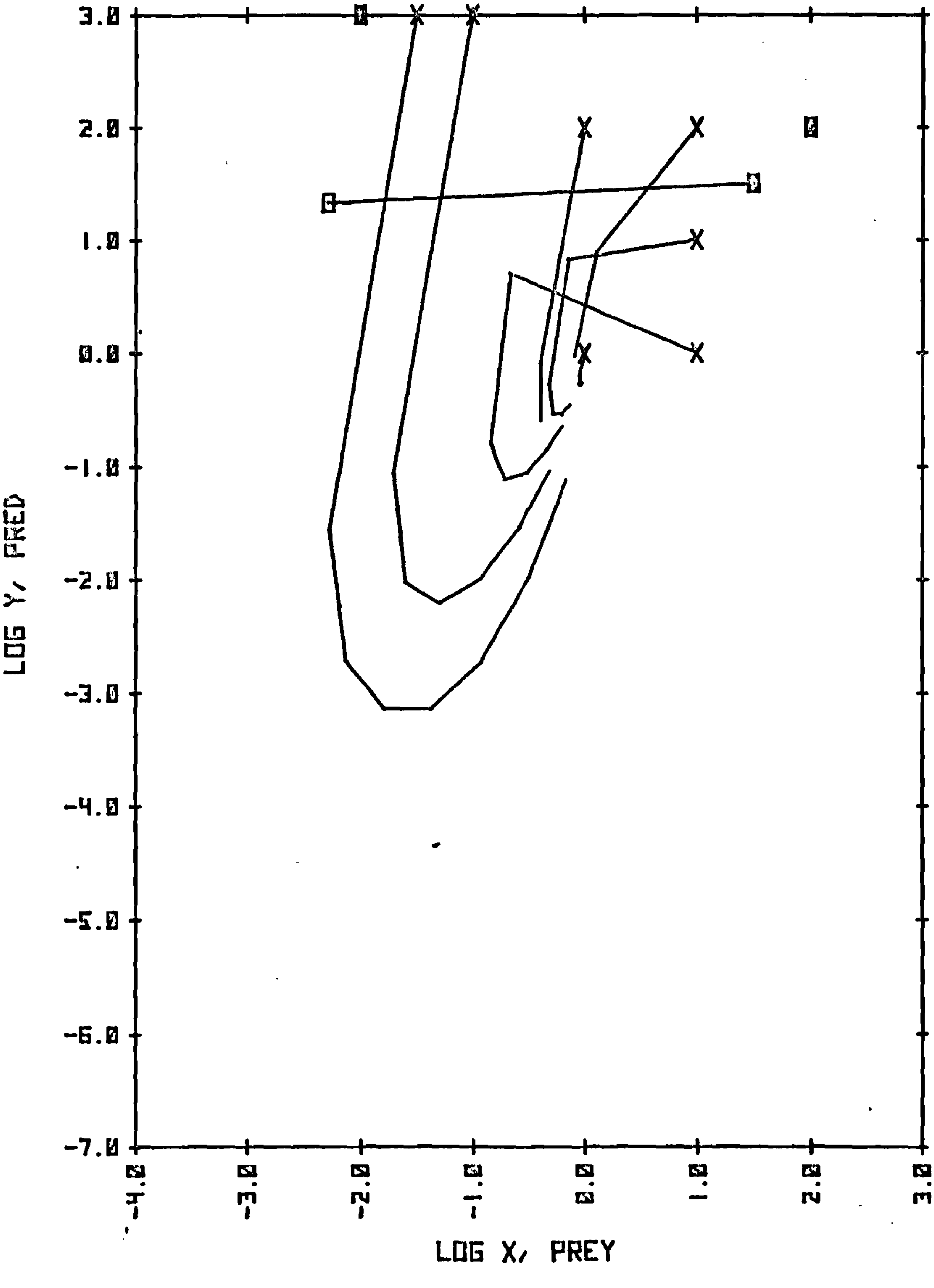

Figure 4c. Sample Phase Plane Trajectory for C = 0 and k = 0.6

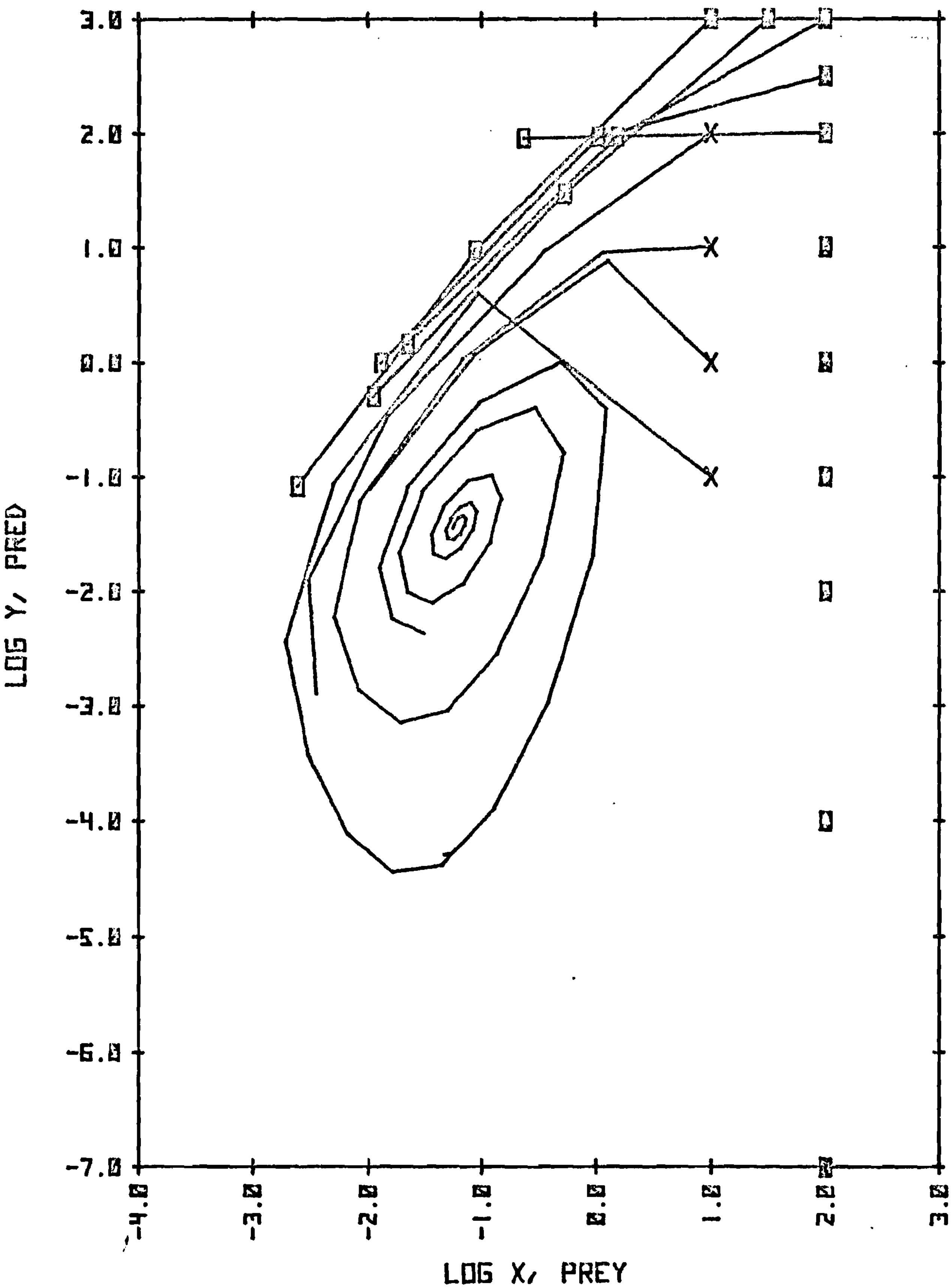

Figure 4d. Sample Phase Plane Trajectory for C = 0 and k = 0.825

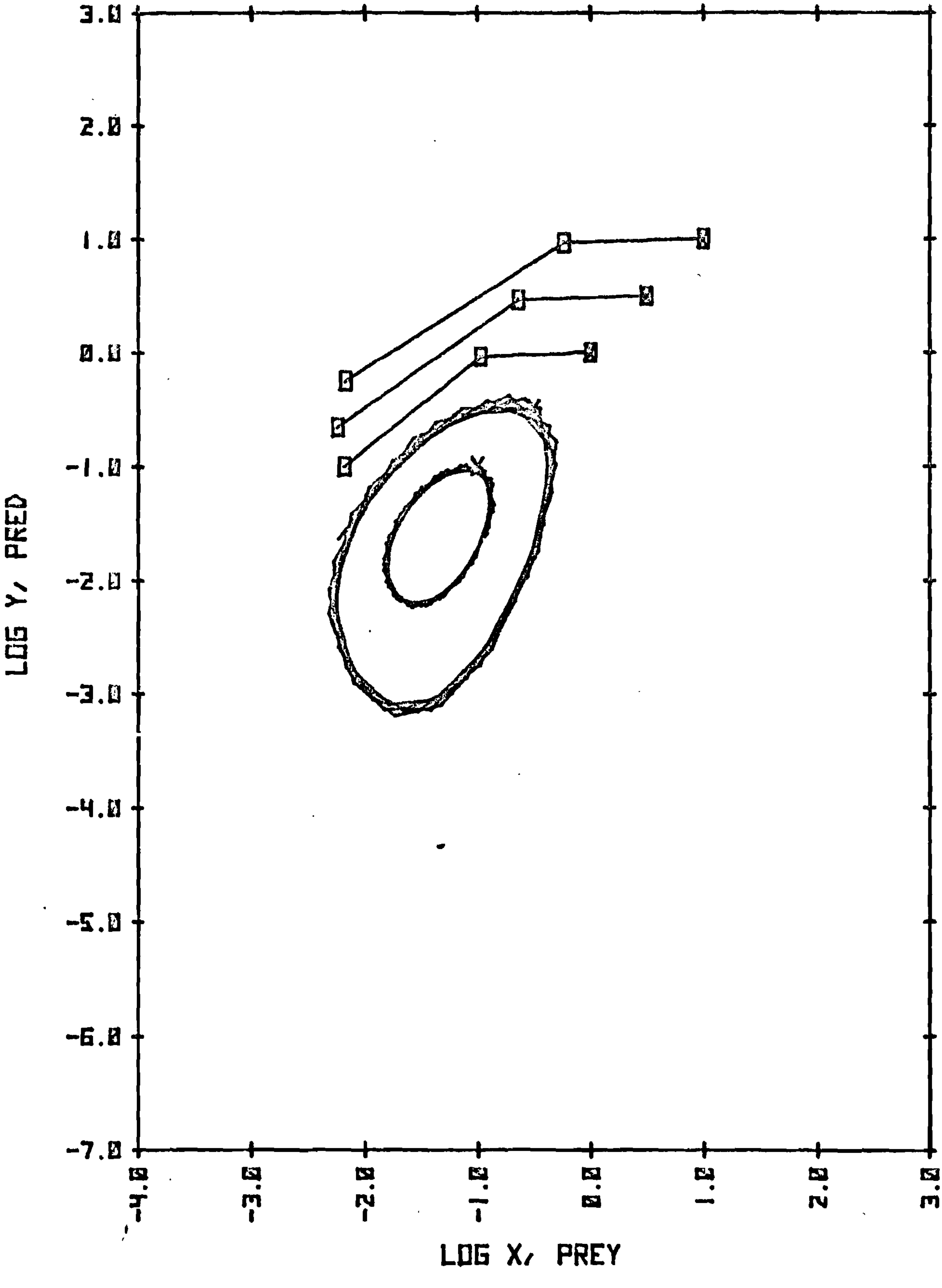

Figure 4e. Sample Phase Plane Trajectory for C = 0 and k = 1.0

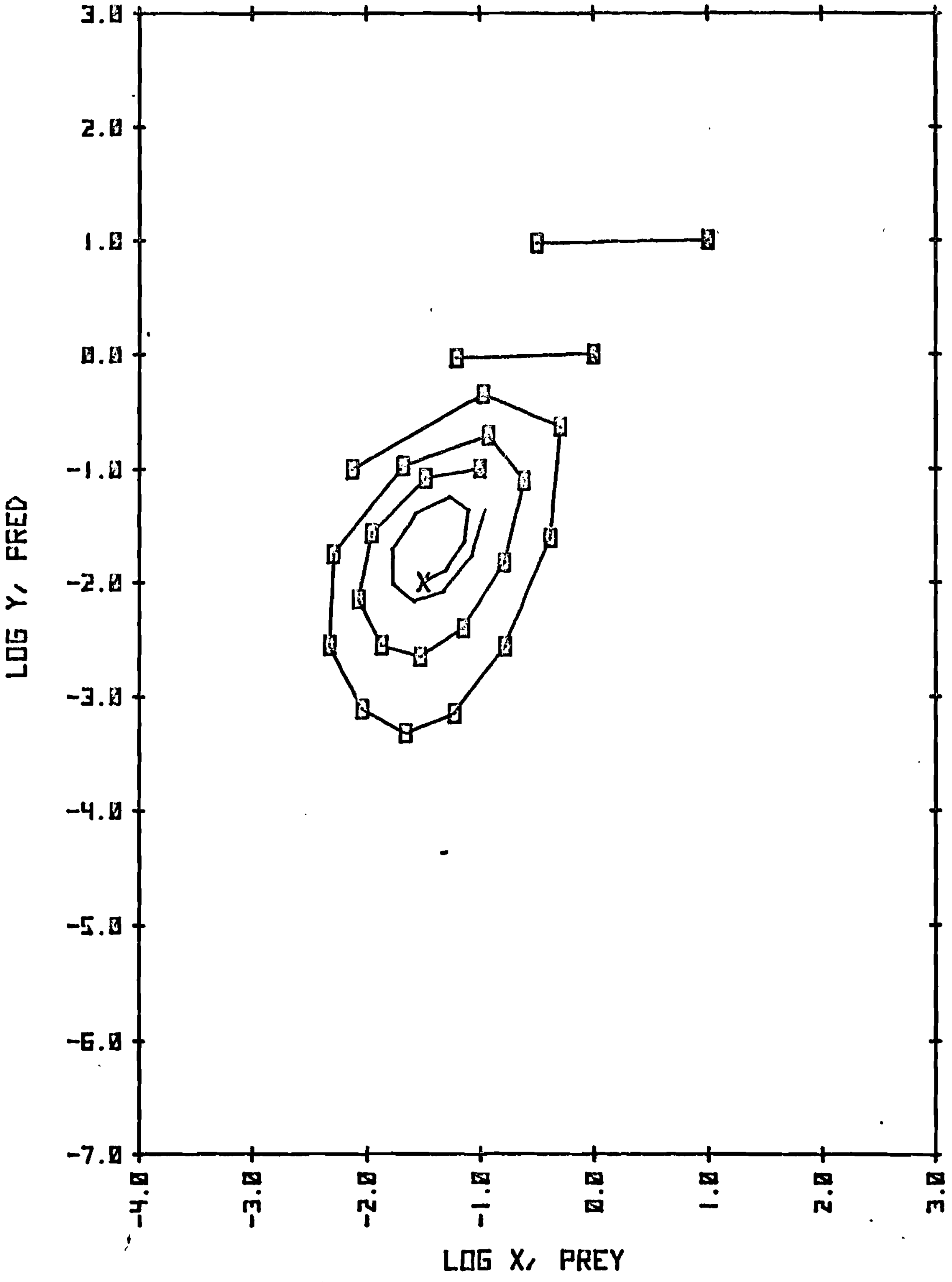

Figure 4f. Sample Phase Plane Trajectory for C = 0 and k = 1.4

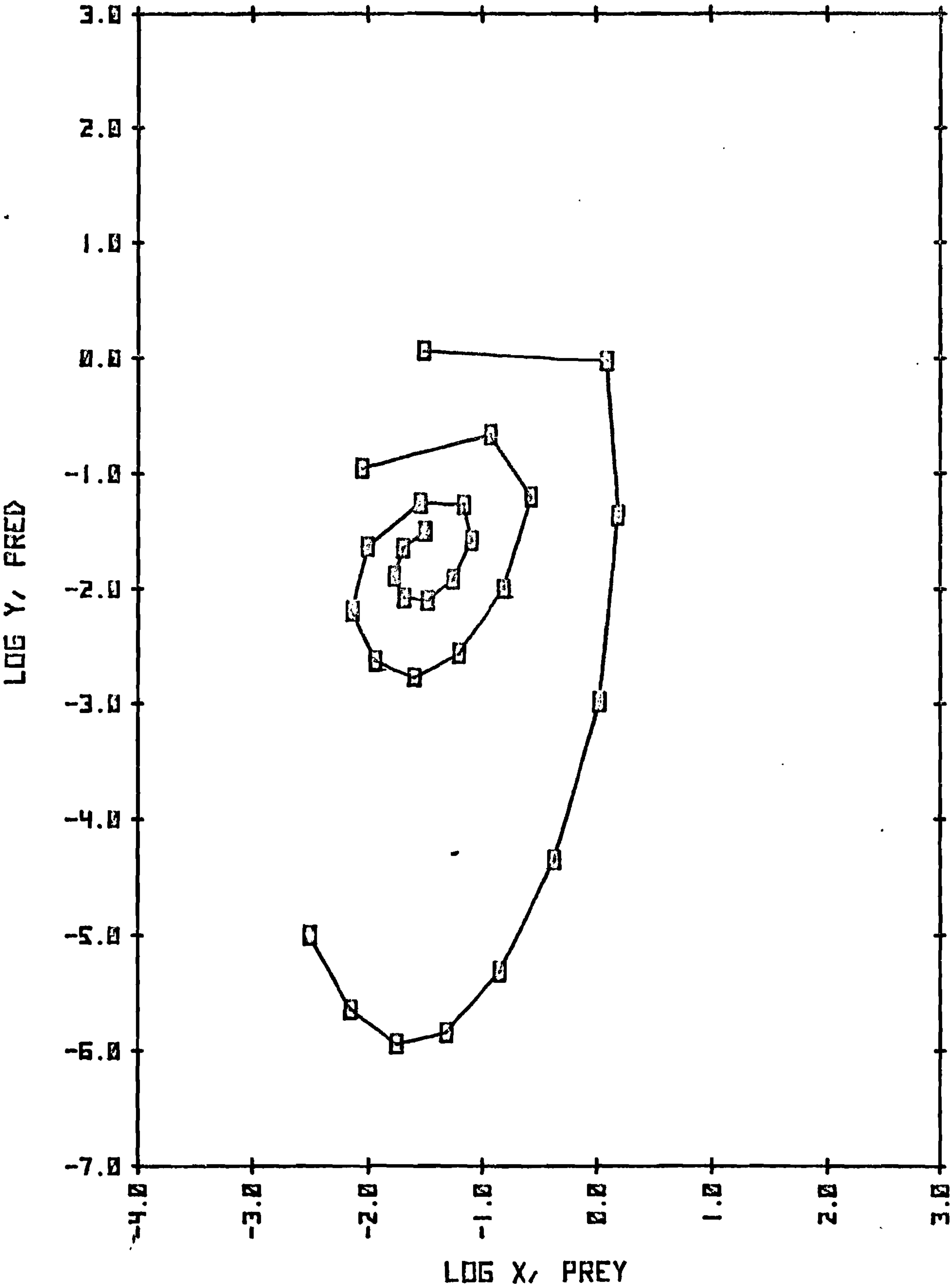

Figure 5a. Sample Phase Plane Trajectory for C = 1 and k = 0.6

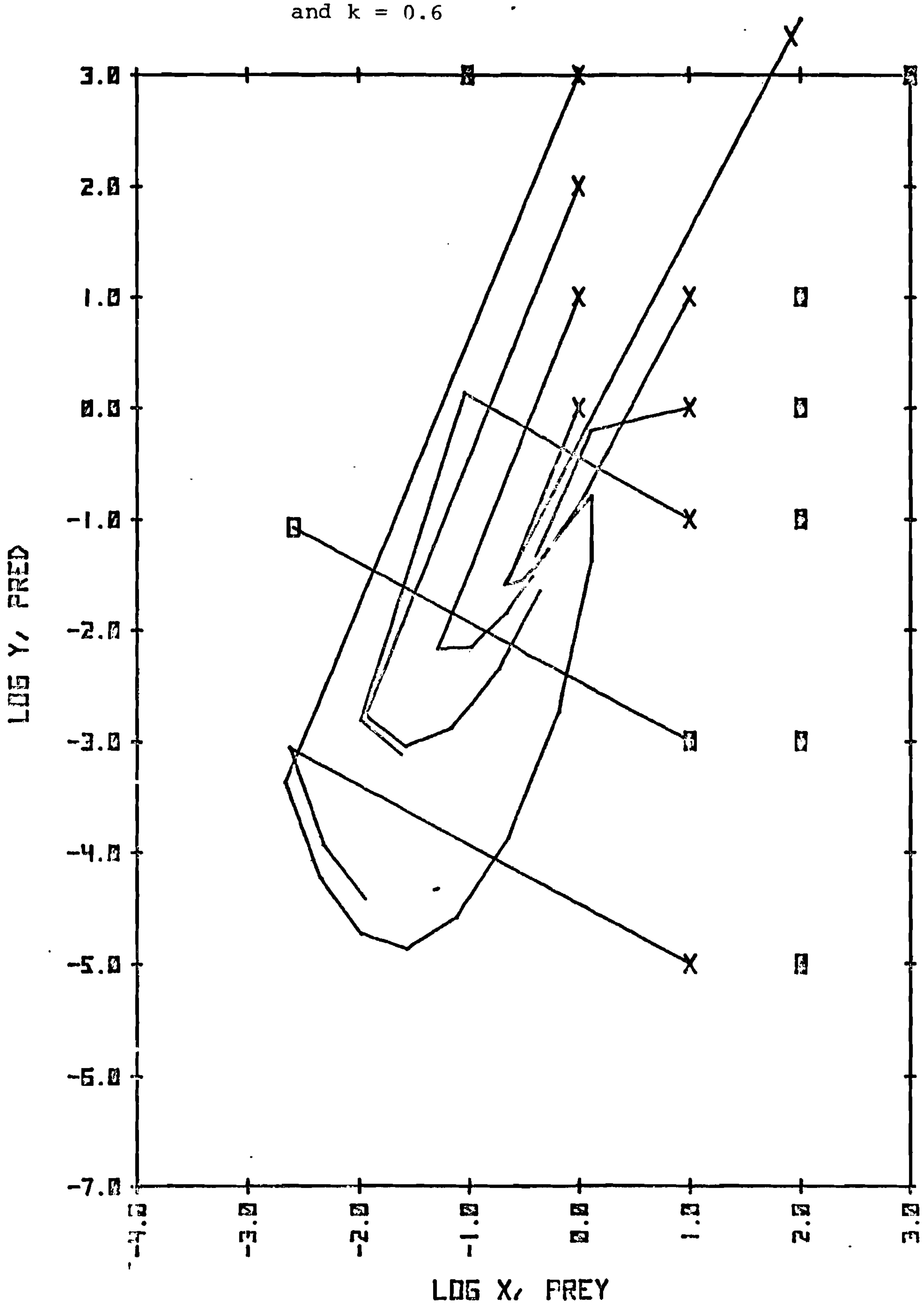

Figure 5b. Sample Phase Plane Trajectory for C = 1
and k = 1.8

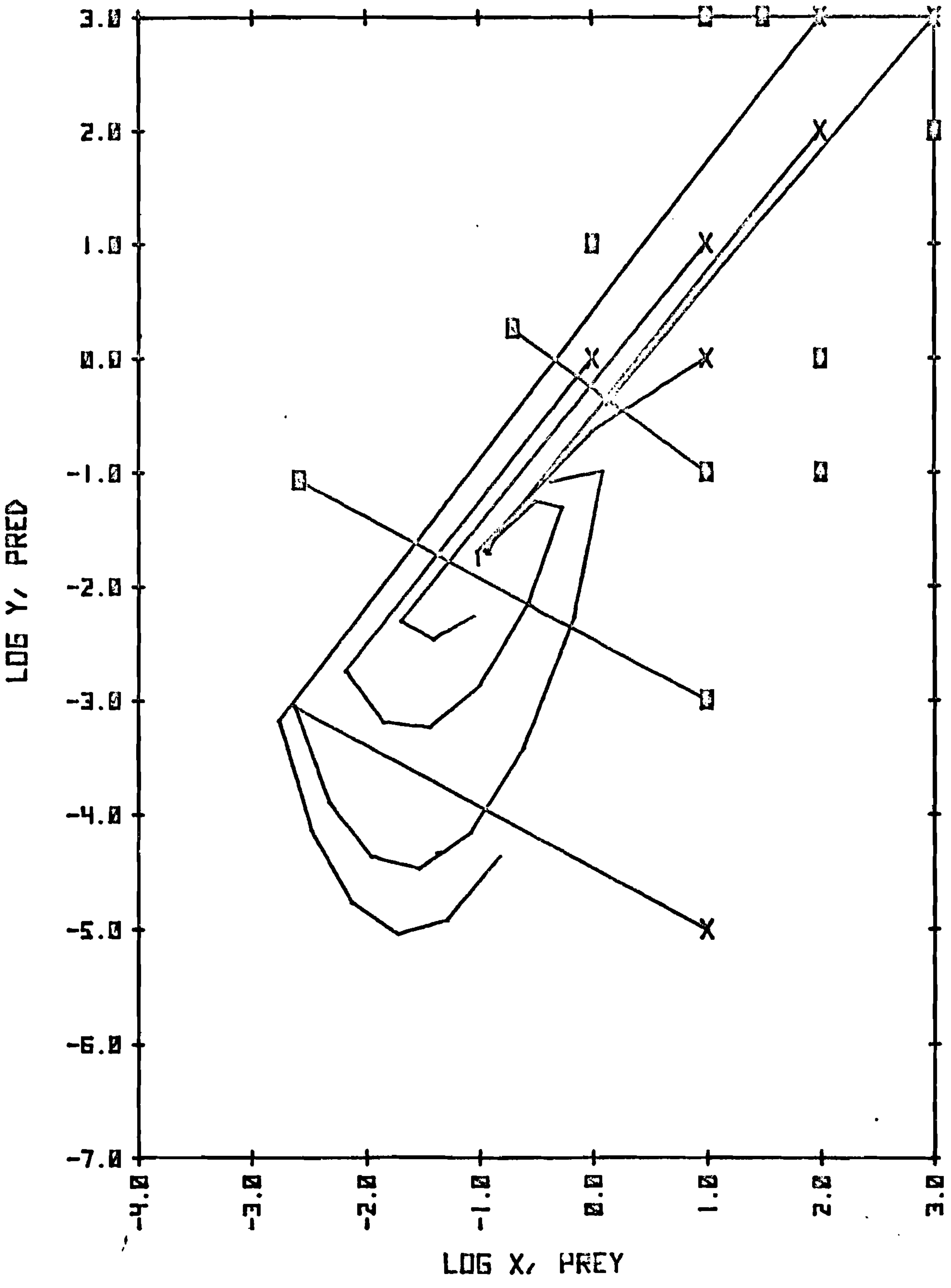

Figure 5c. Sample Phase Plane Trajectory for C = 1 and k = 3.0

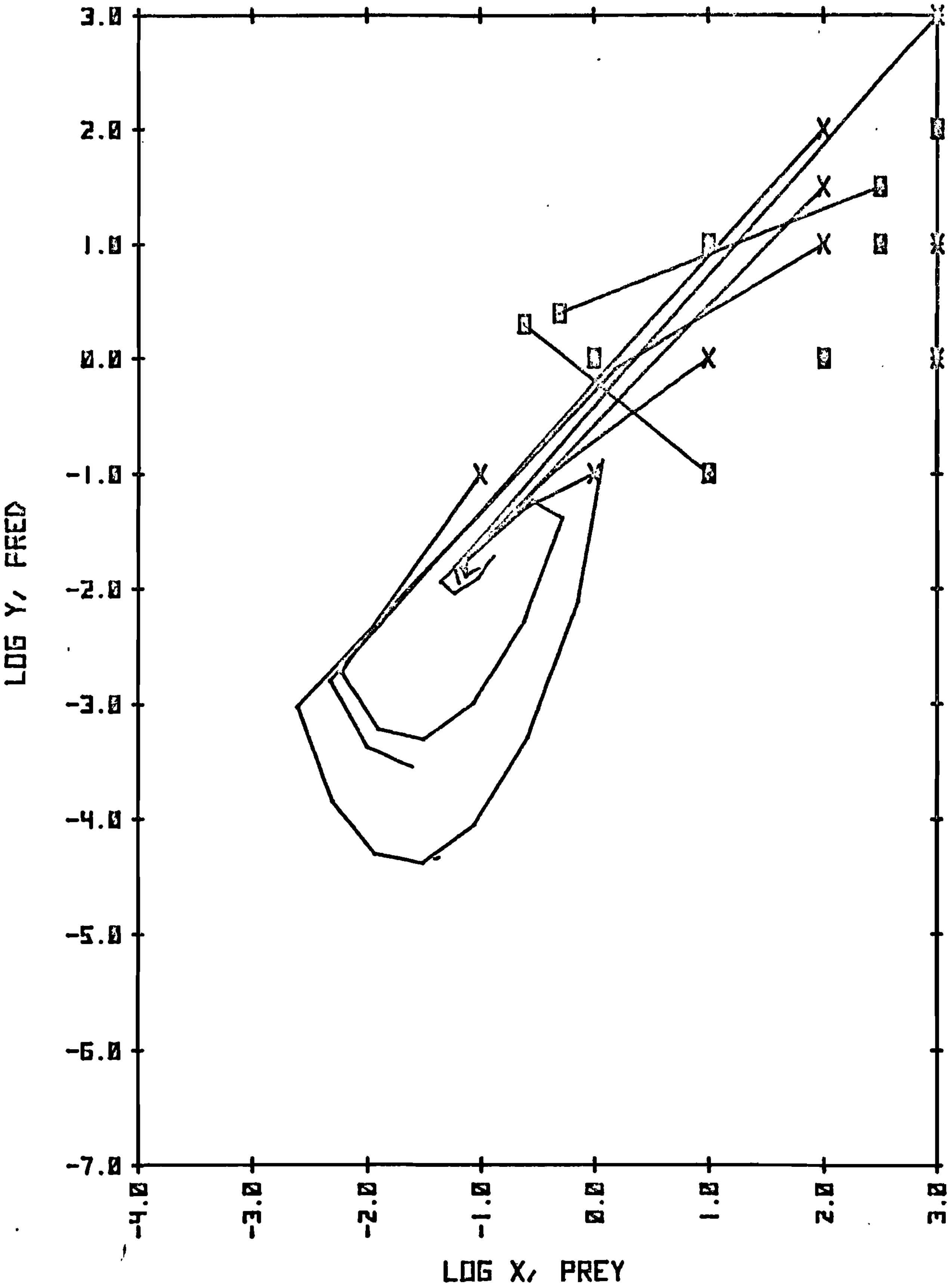

Figure 5d. Sample Phase Plane Trajectory for C = 1 and d = 6.0

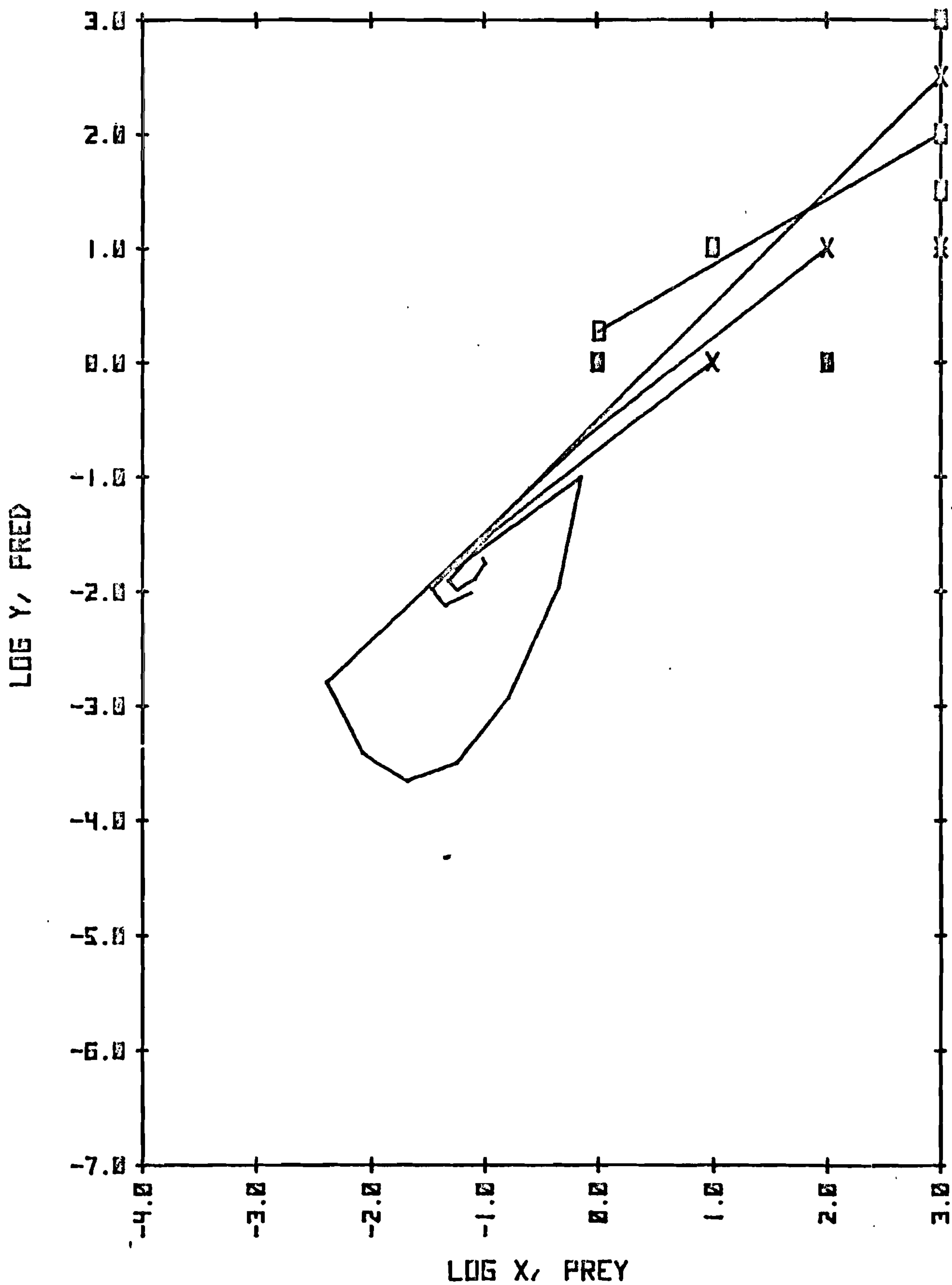

Figure 5e. Sample Phase Plane Trajectory for C = 1 and k = 10

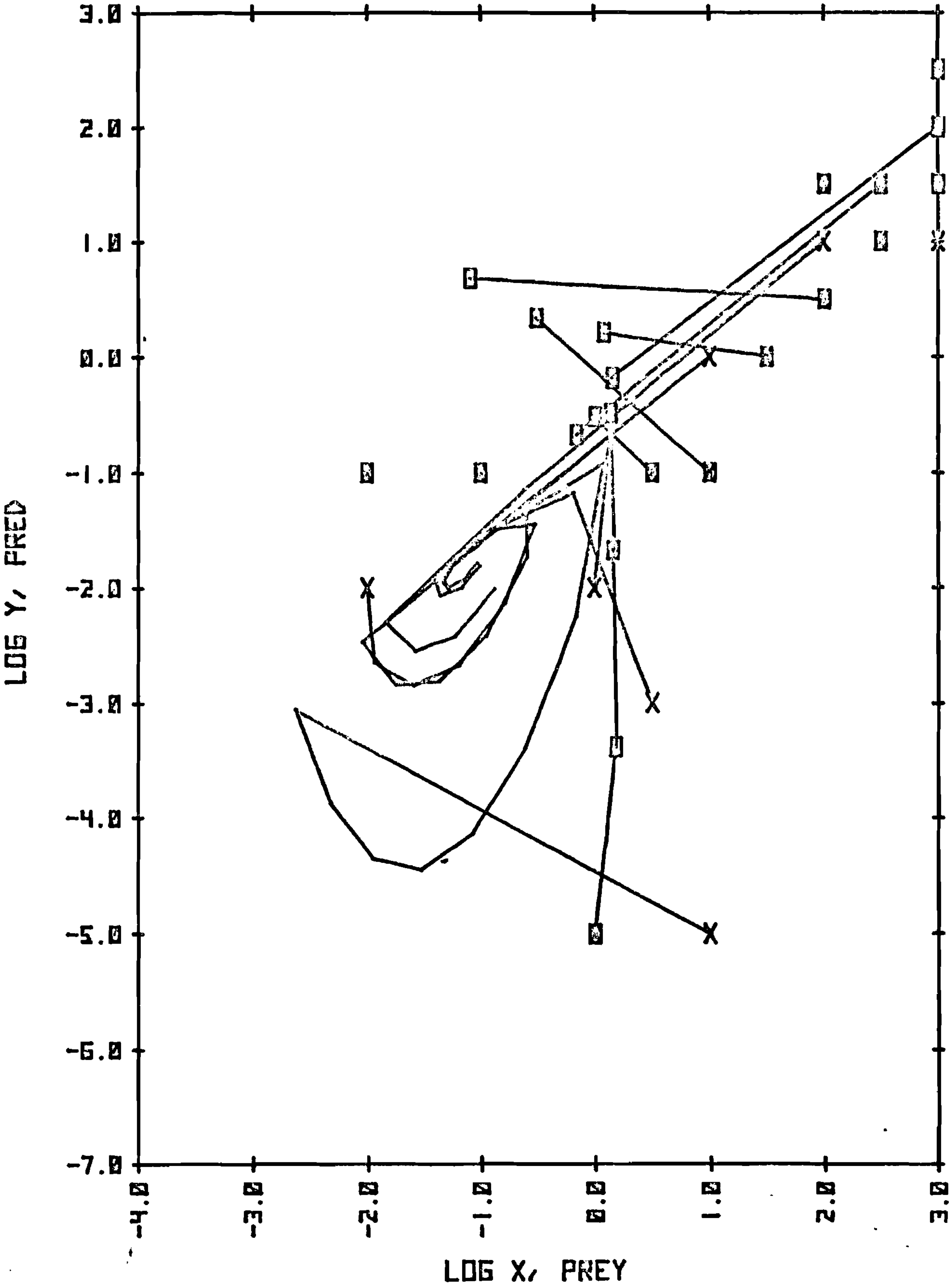

Figure 5f. Sample Phase Plane Trajectory for C = 1 and k = 100