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*An Analysis of a Discrete Age-Structured
Prey-Predator Model*

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From Chaos to Chaos.
An Analysis of a Discrete Age-Structured
Prey–Predator Model

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Abstract

Discrete age-structured density dependent one-population models and discrete age-structured density dependent prey–predator models are considered. Regarding the former, we present formal proofs of the nature of bifurcations involved as well as presenting some new results about the dynamics in unstable and chaotic parameter regions. Regarding the latter, we show that increased predation may act both as a stabilizing and a destabilizing effect. Moreover, we find that possible periodic dynamics of low period, either exact or approximate, may not be generated by the predator, but it may be generated by the prey. Finally, what is most interesting from the biological point of view, is that increased predation is not capable of altering the periodicity of initial low periodic dynamics of the prey in any substantial way, provided the populations are in unstable parameter regions.

1 Introduction

The use of nonlinear matrix models as a powerful tool in the description of various properties of a population with non-overlapping generations (or stages) is well documented in Caswell's and Cushing's books (Caswell 1989, Cushing 1998). Indeed, in consideration of problems within population dynamics, Levin and Goodyear (1980) and later Levin (1981) formulated and analysed their striped bass fishery model in terms of a density dependent Leslie matrix. DeAngelis et al. (1980) and Bergh and Getz (1988) focused on return paths and return times to the stable equilibrium after small perturbations. A logistic matrix model was developed and presented by Liu and Cohen (1987) and applied by Desharnais and Liu (1987) on the flour beetle *Tribolium castaneum*.

Other authors have from a more theoretical point of view paid attention to the qualitative behaviour of an age-structured population in unstable and chaotic parameter regions, see f.ex. Guckenheimer et al. (1977), Silva and Hallam (1993), Wikan and Mjølhus (1995, 1996) and Wikan (1997). Information on general ergodic properties of nonlinear one-population matrix models may be obtained in Cushing (1988, 1989), and in Crowe (1994), and most interesting, it has recently been demonstrated (Cushing et al. 1996, Dennis et al. 1997, Costantino et al. 1997, Cushing et al. 1998) that 3×3 matrix models indeed may be used in order to predict nonstationary and even chaotic behaviour of laboratory insect populations.

The purpose of this work is two-fold. In one direction we shall state and prove some theorems concerning the nature of bifurcations involved (sub- or supercritical) in some of the most frequently used age-structured one-population models quoted above, and we shall also present new results about the possible dynamics beyond the bifurcation thresholds. In another direction, the purpose of this work is to extend results from the previously quoted papers on one-population models by considering a discrete nonlinear age-structured prey-predator model formulated within the framework of Leslie matrices. The main question which we consider here is to reveal what kind of qualitative dynamical changes a discrete age-structured prey population may undergo as we increase its

interaction with an age-structured predator population. More specific; we have obtained interesting results regarding the following questions:

- (1) Given that the prey, in absence of the predator, exhibits almost periodic chaotic oscillations, what effect (stabilizing or destabilizing) will interaction between the populations have, and what about the periodicity?
- (2) Is it possible to stabilize a “chaotic prey population” if the interaction becomes sufficiently strong?
- (3) The strength of the interaction between the populations is described by an interaction parameter β . Are there qualitative differences of prey–predator cycles found in case of β small (weak interaction) compared to the case where β is large (strong interaction)?

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The plan of the paper is as follows. In Section 2 we present the model. In Section 3 we state and prove theorems concerning the nature of bifurcations involved in the one-population models as well as presenting and analyzing several examples (called Cases 1–4) of age-structured prey–predator interactions. In the analysis we use density-dependent survival probabilities as well as density-dependent fecundity elements. Finally, in Section 4, we discuss and unify results from the previous sections.

2 The Model

Consider the map

$$f : \mathbb{R}^4 \rightarrow \mathbb{R}^4 \quad \bar{z} \rightarrow A\bar{z} \tag{1}$$

where the two-population vector $\bar{z} = (x_1, x_2, y_1, y_2)^T$. x_1 and x_2 , y_1 and y_2 are the 2 age classes of the prey and predator populations respectively. The 4×4 transition matrix A

is on block diagonal form

$$A = \begin{pmatrix} A_1 & 0 \\ 0 & A_2 \end{pmatrix} \quad (2)$$

where each of the blocks have the structure of a Leslie matrix, cf. Caswell (1989) . We define the prey block

$$A_1 = \begin{pmatrix} f_1 & f_2 \\ p & 0 \end{pmatrix} \quad (3)$$

and the predator block

$$A_2 = \begin{pmatrix} g_1 & g_2 \\ q & 0 \end{pmatrix} \quad (4)$$

where f_i and g_i are the fecundity (that is the number of daughters born per female) elements for the prey and predator respectively, and p and q denote the corresponding year-to-year survival probabilities.

In its most general form, we assume that all the matrix elements may be functions of the weighted sums of the age-classes involved, thus $f_i = f_i(u, v)$, $g_i = g_i(u, v)$ and so on, where

$$u = a_1x_1 + a_2x_2 \quad v = b_1y_1 + b_2y_2 \quad (5)$$

Further, we impose the following restrictions

$$\begin{array}{cccc} \frac{\partial f_i}{\partial x_j} \leq 0 & \frac{\partial f_i}{\partial y_j} \leq 0 & \frac{\partial p}{\partial x_j} \leq 0 & \frac{\partial p}{\partial y_j} \leq 0 \\ \frac{\partial g_i}{\partial x_j} \geq 0 & \frac{\partial g_i}{\partial y_j} \leq 0 & \frac{\partial q}{\partial x_j} \geq 0 & \frac{\partial q}{\partial y_j} \leq 0 \\ i = 1, 2 & j = 1, 2 & & \end{array} \quad (6)$$

which biologically means that intra specific competition (for example crowding) leads to a decrease of the fecundity and survival for both species, and that inter specific competition (predation) leads to a decrease of the survival and fecundity of the prey and to an increase of the survival and fecundity of the predator. Finally, in the absence of nonlinearities (self-regulation effects and prey-predator interactions), we have $f_i = F_i(0,0)$, $p = P(0,0)$, $g_i = G_i(0,0)$, $q = Q(0,0)$, where capital letters indicate density independent

elements, and we define the inherent net reproductive number of the prey and predator respectively as $F_1 + PF_2$ and $G_1 + QG_2$ and we further assume that

$$F_1 + PF_2 > 1 \quad G_1 + QG_2 < 1 \quad (7)$$

Finally, using the notation $\bar{x} = (x_1, x_2)^T$, $\bar{y} = (y_1, y_2)^T$, if $\bar{y} = \bar{0}$ we observe that map (1) degenerates to the “prey” map

$$g : \mathbb{R}^2 \rightarrow \mathbb{R}^2 \quad \bar{x} \rightarrow A_1 \bar{x} \quad (8)$$

which has been extensively studied elsewhere in the literature, cf. the papers quoted in the Introduction section. In the next section we shall deal with both (8) and the “full” model (1).

3 Examples

Let us first consider some examples where the density dependence is in the fecundity terms and not in the year-to-year survival probabilities, a choice which has often been used in fishery models. This is based upon the fundamental assumption that most density effects occur within the first year of life, cf. Levin and Goodyear (1980), Bergh and Getz (1988).

Case 1

We start with the prey map

$$(x_1, x_2) \rightarrow (F_1(1 - \gamma x_2)^{1/\gamma} x_1 + F_2(1 - \gamma x_2)^{1/\gamma} x_2, Px_1) \quad (9)$$

where the fecundities are of the Deriso-Schnute form (Bergh and Getz 1988, Tuljapurkar et al. 1994) and $\gamma \leq 0$. Note that $\gamma \rightarrow 0$ gives the well-known Ricker case $F_i e^{-x_2}$, $\gamma = -1$ gives the Beverton and Holt case $F_1/(1 + x_2)$. In (9) only the second age class contributes to density effects. The more general situation will be considered later. For the map (9) we have the following:

Theorem 1

Consider the map (9) which fixed point is

$$(x_1^*, x_2^*) = \left(\frac{1}{P} x_2^*, \frac{1}{\gamma} [1 - (F_1 + PF_2)^{-\gamma}] \right) \quad (10)$$

Suppose $-(1 + \sigma P)/(1 + 2\sigma P) < \gamma \leq 0$ where $F_2 = \sigma F_1$.

Then, for fixed values of γ , σ and P , (x_1^*, x_2^*) will undergo a supercritical Hopf bifurcation at the threshold

$$F_1 = F_H = \frac{1}{1 + \sigma P} \left[1 + \gamma \frac{1 + 2\sigma P}{1 + \sigma P} \right]^{1/\gamma} \quad (11)$$

Proof:

See Appendix B.

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From Theorem 1 we conclude that in case of $F_1 > F_H$, $|F_1 - F_H|$ small, there exists an attracting invariant curve surrounding the unstable fixed point (x_1^*, x_2^*) . Now, following Guckenheimer and Holmes (1990), on that curve (9) is topological equivalent to a circle map

$$\theta \rightarrow \theta + c + br^2 + \text{higher order terms} \quad (12)$$

where $c = |\arg \lambda|$, (λ is the dominant eigenvalue computed from the eigenvalue equation of the linearized map), gives asymptotic information of the rotation number associated with the circle map. Now, at our bifurcation threshold (11) the eigenvalue equation may be written as

$$\lambda^2 - \frac{1}{1 + \sigma P} \lambda + 1 = 0 \quad (13)$$

with solution

$$\lambda = \frac{1}{2(1 + \sigma P)} \left\{ 1 \pm \sqrt{4(1 + \sigma P)^2 - 1} i \right\}$$

Unless $\sigma \gg 1$ the location of the eigenvalues clearly suggests that there will be no frequency locking into an exact periodic orbit. If $\sigma \gg 1$, λ is located close to the imaginary axis but unlike the situation discussed in Wikan and Mjølhus (1995) where $\text{Re } \lambda < 0$ we have found no tendency towards 4-periodic dynamics here. Hence, the only outcome in the unstable parameter region is a quasistationary orbit.

This is exemplified in Figures 1a and 1b where we have shown the dynamics beyond the bifurcation threshold for the map

$$(x_1, x_2) \rightarrow (F_1 e^{-x_2} x_1 + F_2 e^{-x_2} x_2, P x_1) \quad (14)$$

(cf. (9)) for different choices of the fecundity F_1 . In Figure 1a ($F_1 = 2.5$) we see the invariant curve just beyond the bifurcation threshold, in Figure 1b ($F_1 = 5.0$) we show the attractor in the chaotic regime and we have found no example of periodic orbits.

Our next goal is to investigate what kind of qualitative dynamical changes the prey population may undergo as we introduce the interaction with the predator population into the model. In order to do so we consider the map:

$$(x_1, x_2, y_1, y_2) \rightarrow (F_1 e^{-(x_2 + \beta_1 y_2)} x_1 + F_2 e^{-(x_2 + \beta_1 y_2)} x_2, P x_1, G_1 e^{-y_2} \frac{\beta_2 x_2}{1 + \beta_2 x_2} y_1 + G_2 e^{-y_2} \frac{\beta_2 x_2}{1 + \beta_2 x_2} y_2, Q y_1) \quad (15)$$

that is, we consider the case where both species consist of 2 age-classes and that both species have intra specific interactions of the Ricker type. Moreover, the model expresses that the prey is exposed to predation from the second age-class of the predator (y_2) and that the fecundity of the predator is related to the second age-class of the prey. Both species have constant year-to-year survival probabilities. Finally, there are two non-negative parameters β_1 and β_2 which will be referred to as the coupling or the interaction parameters and obviously if $\beta_1 = \beta_2 = 0$, (15) degenerates to the pure prey map (14).

The unique nontrivial fixed point of (15) is

$$(x_1^*, x_2^*, y_1^*, y_2^*) = \left(\frac{1}{P} x_2^*, x_2^*, \frac{1}{Q} y_2^*, y_2^* \right) \quad (16)$$

where

$$y_2^* = \frac{1}{\beta_1} [\ln(F_1 + P F_2) - x_2^*] \quad (17)$$

and x_2^* is uniquely determined by

$$x_2^* - \ln(F_1 + PF_2) = \beta_1 \ln \left[\frac{1 + \beta_2 x_2^*}{\beta_2 x_2^* (G_1 + QG_2)} \right] \quad (18)$$

Note that in the case $\beta_1 = \beta_2 = \beta \rightarrow 0$, then $x_2^* > \ln(F_1 + PF_2)$ which implies that y_2^* is negative. Biologically this simply means that there exists a threshold β_E which β must exceed in order for the predator to survive so in the following we shall assume that $\beta > \beta_E$.

Using standard linearization techniques, the eigenvalue equation may, after some algebra, be cast in the form

$$\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0 \quad (19)$$

where

$$\begin{aligned} a_1 &= -\frac{F_1}{F_1 + PF_2} - \frac{G_1}{G_1 + QG_2} \\ a_2 &= x_2^* + y_2^* - \frac{PF_2}{F_1 + PF_2} - \frac{QG_2}{G_1 + QG_2} + \frac{F_1 G_1}{(F_1 + PF_2)(G_1 + QG_2)} \\ a_3 &= -\frac{G_1 x_2^*}{G_1 + QG_2} - \frac{F_1 y_2^*}{F_1 + PF_2} + \frac{PF_2 G_1 + F_1 QG_2}{(F_1 + PF_2)(G_1 + QG_2)} \\ a_4 &= x_2^* y_2^* - \frac{PF_2 y_2^*}{F_1 + PF_2} - \frac{QG_2 x_2^*}{G_1 + QG_2} + \frac{PQG_2 G_2}{(F_1 + PF_2)(G_1 + QG_2)} + \beta_1 \frac{y_2^*}{1 + \beta_2 x_2^*} \end{aligned}$$

By use of the Jury criteria (Murray 1993) it is straightforward to show that the fixed point (16) will never undergo a saddle node or a flip bifurcation at instability threshold since the expressions

$$1 + a_1 + a_2 + a_3 + a_4 = x_2^* y_2^* + \beta_1 \frac{y_2^*}{1 + \beta_2 x_2^*} \quad (20a)$$

$$\begin{aligned} 1 - a_1 + a_2 - a_3 + a_4 &= \left(1 + y_2^* + \frac{G_1 - QG_2}{G_1 + QG_2} \right) x_2^* \\ &+ \left(1 + \frac{F_1 - PF_2}{F_1 + PF_2} \right) y_2^* + \frac{4F_1 G_1}{(F_1 + PF_2)(G_1 + QG_2)} + \beta_1 \frac{y_2^*}{1 + \beta_2 x_2^*} \end{aligned} \quad (20b)$$

both are positive. Thus stability or oscillations due to a Hopf bifurcation are the only possible outcomes, so in some respects we do not expect substantial changes of the dynamics in model (15) compared to what was found in the ‘‘pure’’ prey model (14).

Now, in order to examine this closer we apply the following strategy. We adjust the prey parameters F_1 , F_2 and P in such a way that the prey in absence of the predator exhibits chaotic oscillations. Then we start to increase the coupling parameter $\beta = \beta_1 = \beta_2$ (the case $\beta_1 \neq \beta_2$ will be considered later) which in turn leads to an increase of the equilibrium population of the predator (since the result of (18) inserted in (17) gives that y_2^* is an increasing function of β), and search for qualitative changes of the prey dynamics.

For small values of β , the system is still in the chaotic regime and the chaotic attractor is qualitatively similar to the one shown in Figure 1b, but as β is further enlarged this attractor disappears and the dynamics found is a quasiperiodic orbit restricted on an invariant curve. This is exemplified in Figure 2a. (Parameter values $F_1 = 3$, $F_2 = 5$, $P = 0.6$, $G_1 = G_2 = 2$, $Q = 0.9$, $\beta = 0.40$.)

Keeping the other parameters fixed, our finding is that the fixed point (16) becomes stable when β is increased to a threshold β_L so what our analysis demonstrates is that in this part of parameter space, an increase of the interaction parameter β acts as a stabilizing effect. (Using the parameter values above we find that $\beta_L = 0.42$ with corresponding modulus 1 eigenvalues $\lambda = 0.2486 \pm 0.9740i$.)

The fixed point (16) is stable on an interval $\beta_L < \beta < \beta_H$, but as $\beta \rightarrow \beta_H$ the magnitude of the dominant eigenvalues starts to increase again which signals that we have now entered a part of parameter space where an increase of β acts as a destabilizing effect. At β_H , (16) undergoes a new Hopf bifurcation so whenever $\beta > \beta_H$, $|\beta - \beta_H|$ small, the dynamics is once again restricted on an invariant curve and we have found no example of periodic or almost periodic orbits on that curve. This is shown in Figure 2b where $\beta = 1.32$. (With our choice of parameter values, $\beta_H = 1.30$ and $\lambda = 0.733183 \pm 0.681146i$.) A summary of the dynamics presented above is given in a bifurcation diagram, cf. Figure 3.

Case 2

Consider the map,

$$(x_1, x_2, y_1, y_2) \rightarrow \left(F_1 e^{-(x+\beta_1 y)} x_1 + F_2 e^{-(x+\beta_1 y)} x_2, P x_1, \right. \\ \left. G_1 e^{-y} \frac{\beta_2 x}{1 + \beta_2 x} y_1 + G_2 e^{-y} \frac{\beta_2 x}{1 + \beta_2 x} y_2, Q y_1 \right) \quad (21)$$

Note that the only difference between (21) and (15) is that the fecundity functions in (21) depend on the total populations $x = x_1 + x_2$ and $y = y_1 + y_2$, not on x_2 and y_2 only. As it will become clear this difference has substantial dynamical consequences.

In case of no predation, map (21) degenerates to the well-known one-population model

$$(x_1, x_2) \rightarrow (F e^{-x} x_1 + F e^{-x} x_2, P x_1) \quad (22)$$

the Ricker case, with the restriction $F_1 = F_2 = F$. The reason behind this restriction is that the dynamics found in the case $F_1 \ll F_2$ differs substantially from the cases $F_1 \approx F_2$ and $F_1 > F_2$ (Wikan and Mjølhus 1996), so in order to limit the number of cases to discuss we consider here the case $F_1 = F_2$ only.

Map (22) is a special case of

$$(x_1, x_2) \rightarrow (F(1 - \gamma x)^{1/\gamma} x_1 + F(1 - \gamma x)^{1/\gamma} x_2, P x_1) \quad (23)$$

and in consideration of the latter we have the following:

Theorem 2

Consider the map (23) which equilibrium solution is given by

$$(x_1^*, x_2^*) = \left(\frac{1}{1+P} x^*, \frac{P}{1+P} x^* \right) \quad (24)$$

where

$$x^* = \frac{1}{\gamma} [1 - (P + PF)^{-\gamma}] \quad (25)$$

Then:

- (A) For a fixed P , $0 < P < \frac{1}{2}$ and a fixed $\gamma > -\frac{1}{2}(1 - P)$, (x_1^*, x_2^*) will undergo a supercritical flip bifurcation at the threshold

$$F = \frac{1}{1+P} \left[1 + \gamma \frac{2}{1-P} \right]^{1/\gamma} \quad (26)$$

(B) For a fixed P , $\frac{1}{2} < P < 1$ and a fixed $\gamma > -P/(1 + 2P)$, (x_1^*, x_2^*) will undergo a supercritical Hopf bifurcation at the threshold

$$F = \frac{1}{1+P} \left[1 + \gamma \frac{1+2P}{P} \right]^{1/\gamma} \quad (27)$$

Proof:

Cf. Appendix A.

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In consideration of (22), the impact of Theorem 2 is that the fixed point of (22) will undergo a supercritical flip bifurcation at the threshold

$$F = F_F = \frac{1}{1+P} e^{2/(1-P)} \quad 0 < P < \frac{1}{2} \quad (28a)$$

and a supercritical Hopf bifurcation at the threshold

$$F = F_H = \frac{1}{1+P} e^{(1+2P)/P} \quad \frac{1}{2} < P < 1 \quad (28b)$$

A detailed analysis of the dynamics in the parameter regions beyond F_F and F_H may be obtained in Guckenheimer et al. (1977), Levin (1981) and in Wikan and Mjølhus (1996).

Here, we shall only mention that an increase of F beyond the threshold F_F ($0 < P < \frac{1}{2}$) leads to stable orbits with period 2^k , $k = 1, 2, \dots$ and in case of large values of F , even in the chaotic regime a certain kind of periodicity is preserved since the strange attractor consists of 4 separate subsets each of which is visited once every 4th iteration, cf. Wikan and Mjølhus (1996).

On the other hand, in case of P close to unity and $F > F_H$, $|F - F_H|$ small, there exists a stable almost 3-periodic, small amplitude orbit restricted to an invariant curve which is due to the fact that the eigenvalues are close to third root of unity at bifurcation threshold (28b). (If $P = 1$, $\lambda = e^{\pm(2\pi/3)i}$.) For higher values of F there exists an exact large amplitude 3-period orbit which is followed by other periodic orbits of period $2^k \cdot 3$, $k = 1, 2, \dots$ as F is increased. Eventually, for even larger F values, the dynamics becomes

chaotic and in Figure 4a we show what the attractor looks like. Each of the three branches of the attractor are visited only once every 3rd iteration so clearly there is a certain kind of 3-periodicity present in the chaotic regime as well.

Now, in order to reveal what kind of dynamical changes the system will undergo as we introduce the predator we return to map (21).

At equilibrium

$$(x_1^*, x_2^*, y_1^*, y_2^*) = \left(\frac{1}{1+P} x^*, \frac{P}{1+P} x^*, \frac{1}{1+Q} y^*, \frac{Q}{1+Q} y^* \right) \quad (29)$$

The relation between x^* and y^* and the numerical value of x^* may be found by letting $x_2^* = x^*$ and $y_2^* = y^*$ in (17) and (18) respectively.

The coefficients in the eigenvalue equation (19) now becomes

$$\begin{aligned} a_1 &= x_1^* + y_1^* - \frac{F_1}{F_1 + PF_2} - \frac{G_1}{G_1 + QG_2} \\ a_2 &= Px_1^* + Qy_1^* + x_1^*y_1^* \left(1 + \beta_1 \frac{1}{x^*(1 + \beta_2 x^*)} \right) \\ &\quad - \frac{F_1 y_1^* + PF_2}{F_1 + PF_2} - \frac{G_1 x_1^* + QG_2}{G_1 + QG_2} + \frac{F_1 G_1}{(F_1 + PF_2)(G_1 + QG_2)} \\ a_3 &= x_1^* y_1^* (P + Q) \left[1 + \beta_1 \frac{1}{x^*(1 + \beta_2 x^*)} \right] - \frac{(PF_2 + QF_1)y_1^*}{F_1 + PF_2} \\ &\quad - \frac{(PG_1 + QG_2)x_1^*}{G_1 + QG_2} + \frac{PG_1 F_2 + QF_1 G_2}{(F_1 + PF_2)(G_1 + QG_2)} \\ a_4 &= PQx_1^* y_1^* \left(1 + \beta_1 \frac{1}{x^*(1 + \beta_2 x^*)} \right) - \frac{PQF_2 y_1^*}{F_1 + PF_2} \\ &\quad - \frac{PQG_2 x_1^*}{G_1 + QG_2} + \frac{PQF_2 G_2}{(F_1 + PF_2)(G_1 + QG_2)} \end{aligned} \quad (30)$$

Obviously, as in Case 1 the fixed point (29) will not undergo a saddle node bifurcation since (cf. (20a))

$$1 + a_1 + a_2 + a_3 + a_4 = x^* y^* \left[1 + \beta_1 \frac{1}{x^*(1 + \beta_2 x^*)} \right] > 0 \quad (31)$$

The criterion for (29) not to undergo a flip bifurcation is

$$\begin{aligned} &y^* \frac{(1-Q)}{(1+Q)} \left\{ x^* \frac{(1-P)}{(1+P)} \left[1 + \beta_1 \frac{1}{x^*(1 + \beta_2 x^*)} \right] - \frac{2F_1}{F_1 + PF_2} \right\} > \\ &\frac{2G_1}{G_1 + QG_2} \left\{ \frac{(1-P)}{(1+P)} x^* - \frac{2F_1}{F_1 + PF_2} \right\} \end{aligned} \quad (32)$$

and here one may observe the following: First, suppose that $P \rightarrow 0$, β_1, β_2 are small and F_1 is large. Then x^* is large and y^* is small, and clearly, the implication of this is that the inequality sign in (32) is reversed. On the other hand, suppose that β_1 and β_2 becomes larger which in turn implies that x^* becomes smaller and y^* larger. Then it is easy to see that the left hand side of (32) is greater than the right hand side. This demonstrates that in case of small values of P (29) may undergo a flip bifurcation for sufficiently large values of β_1 and β_2 .

Next, suppose that $P \rightarrow 1$, then (roughly!) (32) may be written as

$$\frac{1-Q}{1+Q} y^* < \frac{2G_1}{G_1 + QG_2} \quad (33)$$

which is valid unless y^* becomes very large. (If $Q \rightarrow 1$ (33) is obviously valid.) Hence we do not expect (29) to go through a flip bifurcation for large values of P , so what these findings indicate is that in case of P is small, the transfer from stability to instability goes through a flip bifurcation and in case of P large stability or nonstationarity dynamics due to a (supercritical) Hopf bifurcation are the typical outcomes.

In order to examine this closer we apply the same strategy as in Case 1. Hence, consider the fixed parameter set $F = F_1 = F_2 = 18.5$, $P = 0.9$, $G_1 = G_2 = G = 5.0$, $Q = 0.5$. If $\beta = \beta_1 = \beta_2 = 0$ there is no predation, the prey dynamics is chaotic but still almost 3-periodic as displayed in Figure 4a. For small values of β the structure of the attractor remains unchanged. In Figure 4b we show the situation for the predator in the case $\beta = 0.08$, showing that the predator has been forced into the same kind of periodicity as the prey, cf. the discussion in Boonstra et al. (1998). Further increase of β acts stabilizing since the dynamics now becomes periodic with period $3 \cdot 2^k$, $k = \dots, 3, 2, 1, 0$, thus an increase of β leads to the flip bifurcation sequence in the opposite direction. An exact 3-periodic orbit for both the prey and the predator is shown in Figures 5a,b ($\beta = 0.26$). Stability of the fixed point is achieved when $\beta = \beta_L = 0.29$ where the root of (19) is $\lambda = -0.5407 \pm 0.8462i$. The fixed point (29) is stable whenever $\beta \in [\beta_L, \beta_H]$. With our choice of parameters; $\beta_H = 2.38$ with corresponding modulus 1 eigenvalues $\lambda = 0.4978 \pm 0.8655i$ so evidently there is another Hopf bifurcation at the threshold

β_H . In case of $\beta > \beta_H$, $|\beta - \beta_H|$ small, there is a quasiperiodic orbit with no sign of any periodicity. This is exemplified in Figure 6. For higher values of β the populations reenter a chaotic regime.

—o—

Starting from zero, numerical simulations show that an increase of β in the case of P small gives in many respects much of the same qualitative picture as in the case P large. For small values of β the prey is still in the chaotic regime, and the predator is forced into a chaotic almost 4-period orbit. Further enlargement of the coupling parameter leads also here to the flip bifurcation sequence in the opposite direction giving birth to stable orbits of period 2^k , $k = \dots, 3, 2, 1$. At β_L stability is gained and $\lambda_L = -1$. Stability is maintained in $[\beta_L, \beta_H]$. At the threshold β_H there is a Hopf bifurcation which leads to quasiperiodic behaviour, and eventually the dynamics becomes chaotic. A numerical example: Suppose $F = 58.5$, $P = 0.2$, $G = 5$, $Q = 5$. Then $\beta_L = 0.93$, ($\lambda_L = -1$), $\beta_H = 2.41$, $\lambda_H = 0.2510 \pm 0.9673i$.

Case 3

Consider the map $f : \mathbb{R}^4 \rightarrow \mathbb{R}^4$

$$\begin{aligned} (x_1, x_2, y_1, y_2) \rightarrow & (F_1 e^{-(x+\beta_1 y)} x_1 + F_2 e^{-(x+\beta_1 y)} x_2, P x_1, \\ & G_1 e^{-y} (1 - e^{-\beta_2 x}) y_1 + G_2 e^{-y} (1 - e^{-\beta_2 x}) y_2, Q y_1) \end{aligned} \quad (34)$$

Note that the only difference between the model in Case 2 and the one here is that the prey dependent part in the predator's fecundity terms has been changed. Instead of repeating the same detailed analysis as in Case 2, we shall here summarize the results obtained from (34) in the bifurcation diagram presented in Figure 7 where the parameter values $P = 0.9$, $F_1 = F_2 = 20$, $Q = 0.9$, $G_1 = G_2 = 4$ have been used.

Referring to Figure 7; for small values of $\beta = \beta_1 = \beta_2$ the prey (and the predator) is still in the chaotic regime and we have verified that the attractor is similar to the one shown in Figure 5a. As β is increased stability properties are improved and our analysis

shows that the only stable attractor is a large amplitude exact 3-cycle which is generated by the map $k = f \circ f \circ f$ (cf. (34)). This is followed by a β interval where the 3-cycle coexists with an invariant curve whenever $\beta \in [0.244, 0.26]$ and with the stable fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ in $[0.26, 0.31]$. We have computed numerically that $\beta = \beta_L = 0.26$ as the Jury expression (Murray 1993)

$$|(1 - a_4^2)^2 - (a_3 - a_4 a_1)| - |(1 - a_4^2)(a_2 - a_4 a_2) - (a_3 - a_4 a_1)(a_1 - a_4 a_3)| \quad (35)$$

changes sign and becomes positive. ($a_1 \dots a_4$ are the coefficients in the linearization of (34).) The corresponding modulus 1 eigenvalue is $\lambda_L = -0.5625 \pm 0.8343i$ and since λ_L is close to third root of unity the dynamics on the invariant curve has a strong resemblance of 3-cycles.

Returning to the large amplitude 3-cycle, it is created at the value $\beta = 0.31$ as k undergoes a saddle node bifurcation. (This is verified by substituting a corresponding fixed point $(\bar{x}_1, \bar{x}_2, \bar{y}_1, \bar{y}_2)$ of k into the Jacobian Dk and then observe that the (numerically) computed eigenvalue $u \approx 1$.) The invariant curve disappears when $\beta = 0.244$ as it is “hit” by the three branches of unstable equilibria generated by k . Note that k has seven nontrivial fixed points, cf. Wikan and Mjøhus (1996).

When $\beta = 1.1$ further enlargement acts as a destabilizing effect and at the value $\beta_H = 1.86$, (35) again turns negative which means that $(x_1^*, x_2^*, y_1^*, y_2^*)$ undergoes another Hopf bifurcation ($\lambda_H = 0.4253 \pm 0.9062i$). Beyond β_H the dynamics occurs on an invariant curve whenever $|\beta - \beta_H|$ is small and there is no sign of any periodicity. For higher values of β numerical simulations show that the dynamics once again becomes chaotic.

—o—

If we repeat the analysis above, using small values of P , the same qualitative picture as in the corresponding situation in Case 2 emerges, so instead of presenting details we just mention that there also here exists a stable parameter region $\langle \beta_L, \beta_H \rangle$ and that the eigenvalue at β_L , $\lambda_L = -1$. At β_H the expression (35) fails to be positive, λ_H is found to be complex with $\text{Re } \lambda_H > 0$.

In the next cases we shall give some results about the dynamics found in models where the density dependence is restricted to the survival probabilities.

The basic “prey” map is

$$f : \mathbb{R}^2 \rightarrow \mathbb{R}^2 \quad (x_1, x_2) \rightarrow (F_2 x_2, P(1 - \gamma z)^{1/\gamma} x_1) \quad (36)$$

where $z = \alpha_1 x_1 + \alpha_2 x_2$. Thus, we consider the case where the fecundity is constant and restricted to the last age class only, and we further assume that the survival probability depends of the weighted sum of the two age classes x_1 and x_1 .

Theorem 3

Consider the map (36) under the restrictions $F_2 \neq 2\alpha_2/\alpha_1$, $\alpha_2 \neq 0$. Assume $F_2 > \alpha_2/\alpha_1$. Then for $\gamma > -\alpha_1 F_2 / 2(\alpha_1 F_2 + \alpha_2)$ the fixed point (x_1^*, x_2^*) of map (36) will undergo a supercritical Hopf bifurcation at the threshold

$$P = \frac{1}{F_2} \left(1 - \gamma \frac{2(\alpha_1 F_2 + \alpha_2)}{\alpha_1 F_2} \right)^{1/\gamma} \quad (37)$$

Proof:

See Wikan (1997).

Note that if $\gamma \rightarrow 0$, (36) and (37) may be written as

$$(x_1, x_2) \rightarrow (F_2 x_2, P e^{-z} x_1) \quad (38)$$

$$P = \frac{1}{F_2} e^{2(\alpha_1 F_2 + \alpha_2) / (\alpha_1 F_2)} \quad (39)$$

Following Wikan and Mjølhus (1995), assuming $\alpha_1 = \alpha_2$, the solution of the eigenvalue equation of the linearized map of (38) at bifurcation threshold (39) is

$$\lambda_{\pm} = -\frac{1}{F_2} \pm \frac{1}{F_2} \sqrt{F_2^2 - 1} i \quad (40)$$

and since F_2 is a large number at the threshold (39), λ_{\pm} are located very close to the imaginary axis. Hence, whenever $F_2 > F_{2B}$, $|F_2 - F_{2B}|$ small (where F_{2B} is the F_2 value which satisfies (39) for a given P), the rotation number $\sigma \approx 1/4$ (cf. the discussion just after Theorem 1), thus the dynamics has a strong resemblance of 4-cycles, either exact or approximate.

In somewhat more detail we find that whenever $F_2 - F_{2B}$ small there exists an almost 4-periodic orbit restricted to an invariant curve, as F_2 is increased we obtain an exact 4-period orbit through frequency locking, further enlargement results in the flip bifurcation sequence giving births to orbits of period $4 \cdot 2^k$, $k = 1, 2, \dots$ and beyond the accumulation point for the flip bifurcation sequence the dynamics becomes chaotic. This is shown in Figure 8 and evidently, even in the chaotic regime a certain kind of 4-periodicity is preserved.

If $F_2 \approx 2\alpha_2/\alpha_1$, α_2/α_1 large, λ is close to third root of unity at instability threshold (39), $\sigma \approx 1/3$ so in case of $F_2 > F_{2B}$, in accord with Wikan (1997) the dynamics this time has a strong resemblance of 3-cycles.

Our next goal is to reveal to what extent the inclusion of a predator is capable of altering the periodical behaviour found in the prey models (36) and (38).

Case 4

Consider the map

$$(x_1, x_2, y_1, y_2) \rightarrow \left(F_2 x_2, P e^{-(x+\beta_1 y)} x_1, G_2 y_2, \frac{Q}{1+y} \frac{\beta_2 x}{1+\beta_2 x} y_1 \right) \quad (41)$$

Hence, we assume that the fecundities for both species are constant and restricted to the second age classes only and that the survival probabilities for both populations depend on the total prey as well as the total predator populations. The equilibrium solution of (41) is:

$$x_1^* = \frac{F_2}{1+F_2} x^* \quad x_2^* = \frac{1}{1+F_2} x^* \quad y_1^* = \frac{G_2}{1+G_2} y^* \quad y_2^* = \frac{1}{1+G_2} y^* \quad (42)$$

where

$$\begin{aligned} y^* &= \frac{1}{\beta_1} [\ln(PF_2) - x^*] \\ x^* &= \frac{u + \sqrt{u^2 + 4\beta_2 v}}{2\beta_2} \end{aligned} \quad (43)$$

$$u = \beta_2 \ln(PF_2) + (1 - QG_2)\beta_1\beta_2 - 1 \quad v = \ln(PF_2) + \beta_1$$

Observe that $\beta_1 = \beta_2 = 0$ implies that (41) degenerates to the prey map (38) ($\alpha_1 = \alpha_2 = 1$).

The coefficients in the 4th order eigenvalue equation (19) are

$$\begin{aligned} a_1 &= \frac{x_1^*}{F_2} + \frac{y_1^*}{G_2(1+y^*)} \\ a_2 &= x_1^* - 2 + \frac{y_1^*}{1+y^*} + \frac{x_1^*y_1^*}{F_2G_2(1+y^*)} + \frac{\beta_1x_1^*y_1^*}{F_2G_2x^*(1+\beta_2x^*)} \\ a_3 &= -\frac{x_1^*}{F_2} + \frac{\beta_1x_1^*y_1^*}{F_2x^*(1+\beta_2x^*)} + \frac{\beta_1x_1^*y_1^*}{G_2x^*(1+\beta_2x^*)} - \frac{y_1^*}{G_2(1+y^*)} \\ &\quad + \frac{x_1^*y_1^*}{F_2(1+y^*)} + \frac{x_1^*y_1^*}{G_2(1+y^*)} \\ a_4 &= 1 - x_1^* + \frac{\beta_1x_1^*y_1^*}{x^*(1+\beta_2x^*)} - \frac{y_1^*}{1+y^*} + \frac{x_1^*y_1^*}{1+y^*} \end{aligned} \quad (44)$$

and clearly there will be no transfer from stability to instability through a saddle node or flip bifurcation since

$$1 + a_1 + a_2 + a_3 + a_4 = \frac{(1+F_2)(1+G_2)}{F_2G_2} x_1^*y_1^* \left[\frac{\beta_1}{x^*(1+\beta_2x^*)} + \frac{1}{1+y^*} \right] > 0 \quad (45)$$

$$1 - a_1 + a_2 - a_3 + a_4 = \frac{(1-F_2)(1-G_2)}{F_2G_2} x_1^*y_1^* \left[\frac{\beta_1}{x^*(1+\beta_2x^*)} + \frac{1}{1+y^*} \right] > 0 \quad (46)$$

Hence, stability or dynamics governed by Hopf bifurcations are the only possible outcomes.

Starting with $\beta_1, \beta_2 = 0$ and prey parameters as in Figure 9 ($P = 0.6$, $F_2 = 25$), the results here are similar to what was found in Cases 2 and 3. An increase of the coupling parameters acts as a stabilizing effect but as long as the populations are in the unstable parameter region the initial 4-periodic behaviour is not altered in any substantial way. In Figure 9 we show an exact 4-periodic orbit for both species. (If $F_2 \approx 2\alpha_2/\alpha_1$, α_2/α_1

large, we find 3-periodic orbits.) Stability is achieved at a threshold (Hopf!) where the Jury relation (35) becomes positive. The fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ remains stable as long as (35) is positive and

$$y_1^* < \frac{\beta_2 Q G_2 x_1^* x^* (1 + \beta_2 x^*)}{\beta_1 \beta_2 Q G_2 x_1^* - (1 - x_1^*) (1 + \beta_2 x^*)^2} \quad (47)$$

but when β_1, β_2 is increased to a level where the inequality sign in (47) is reversed the fixed point undergoes a new Hopf bifurcation and in all cases investigated the location of the eigenvalues at the threshold given by (47) is very different from the location at the threshold given by (35). Consequently, the low-periodic behaviour found in case of β_1, β_2 small is not found in case of larger values of the coupling parameters. (A numerical example: $\lambda = -0.03058 \pm 0.99934i$ where (35) becomes positive, $\lambda = 0.77621 \pm 0.63334i$ at the threshold (47).) If we continue to increase β_1 and β_2 the populations reenter a chaotic regime. In a bifurcation diagram, Figure 10, we summarize the results presented above.

In order to close Case 4 let us just briefly mention that the results just presented do not seem to depend upon the functions we use in the description of the survival of the predator in map (41). For example we may replace the 4th component

$$y_2 \rightarrow \frac{Q}{1+y} \frac{\beta_2 x}{1+\beta_2 x} y_1$$

by

$$y_2 \rightarrow Q e^{-y} (1 - e^{-\beta_2 x}) y_1 \quad (48)$$

and still obtain qualitatively the same results as above.

—o—

Finally, if we return to the prey map (39), assuming $F_2 \approx 2\alpha_2/\alpha_1$, α_2/α_1 large, which means that it is x_2 which primarily contributes to density effects, we have already mentioned that 3-periodic behaviour is the outcome beyond the instability threshold.

This is strongly related to the fact that the eigenvalues of linearized map of (39) at the threshold (40)

$$\lambda = -\frac{\alpha_2}{\alpha_1 F_2} \pm \frac{1}{\alpha_1 F_2} \sqrt{(\alpha_1 F_2)^2 - \alpha_2^2} i \quad (49)$$

are close to third root of unity.

Note, however, that if x_2 exclusively contributes to density effects, map (39) becomes

$$(x_1, x_2) \rightarrow (F_2 x_2, P e^{-x_2} x_1) \quad (50)$$

and for this particular map we have the following: The fixed point of (50)

$$(x_1^*, x_2^*) = (F_2 \ln(P F_2), \ln(P F_2)) \quad (51)$$

is always unstable and from the eigenvalue equation $\lambda^2 + a_1 \lambda + a_2 = 0$ it is straightforward to conclude that it is the flip condition $1 - a_1 + a_2 > 0$ which fails. Hence, it is natural to search for a stable 2-cycle.

The 2nd iterate of (50) may be expressed as

$$\begin{aligned} x_{1,t+2} &= P F_2 e^{-x_{2,t}} x_{1,t} \\ x_{2,t+2} &= P F_2 e^{-x_{2,t+1}} x_{2,t} \end{aligned} \quad (52)$$

Here, one possibility is $x_{2,t} = x_{2,t+1} = \ln(P F_2)$ which gives nothing but the trivial cycle where (51) is the repeating point. Another possibility is to search for a 2-cycle of the form $(A, 0), (0, B)$. Then from (52)

$$A = \frac{1}{P} \ln(P F_2)^2 \quad B = \ln(P F_2)^2 \quad (53)$$

but by use of these values we find that the eigenvalues u of the linearized map of (52) must satisfy

$$(u - P F_2) \left(u - \frac{1}{P F_2} \right) = 0 \quad (54)$$

Hence, the 2-cycle $(A, 0), (0, B)$ is also unstable. In fact, the only dynamics found from map (50) is a divergent sequence of points $((A_1, 0), (0, B_1)), ((A_2, 0), (0, B_2)), \dots$, where $A_j > A_{j-1}, B_j > B_{j-1}$.

Now, if we include a predator, for example through the models:

$$(x_1, x_2, y_1, y_2) \rightarrow \left(F_2 x_2, P e^{-(x_2 + \beta_1 y)} x_1, G_2 y_2, \frac{Q}{1+y} \frac{\beta_2 x}{1 + \beta_2 x} y_1 \right) \quad (55)$$

or

$$(x_1, x_2, y_1, y_2) \rightarrow \left(F_2 x_2, P e^{-(x_2 + \beta_1 y)} x_1, (G_1 y_1 + G_2 y_2) e^{-y} \frac{\beta_2 x}{1 + \beta_2 x}, Q y_1 \right) \quad (56)$$

we obtain qualitatively the same results: In case of sufficiently large values of the interaction parameters it is possible to obtain a stable 2-cycle of the form $(A_1, 0, B_1, B_2)$, $(0, A_2, B_3, B_4)$, but it is not possible to obtain a stable fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$.

4 Discussion

In the previous section we have analysed a selected number of 4-dimensional prey–predator models. Focus has been on the dynamical properties and the role of the predator in unstable parameter regions. Despite the fact that we consider 2-age classes for both species only, the parameter space is huge so care should be taken with respect of drawing too strong conclusions, but before we try to unify parts of the results found in the previous section, let us first examine the consequence(s) of using only one coupling parameter $\beta = \beta_1 = \beta_2$ instead of dealing with the more general case $\beta_1 \neq \beta_2$.

Thus, reconsider Case 1, map (15) and Case 2, map (21) (where we use the same parameters F_i, G_i, P and Q as before ($P = 0.9$ in Case 2)) and let $\beta_1 > \beta_L$ be a fixed number. The result of increasing β_2 (starting with $\beta_2 = 0$) is that the fixed point of maps (15) and (21) becomes stable at a certain threshold β_{L2} . In Table 1 we show some fixed values of β_1 , together with the “new” instability threshold β_{L2} and the corresponding eigenvalues of map (15). (The last row in the table is the “old” situation $\beta_L = \beta_{1L} = \beta_{2L}$.) In Table 2 we consider map (21).

Table 1

β_1	β_{2L}	λ
1.00	0.29	$0.2488 \pm 0.971187i$
0.75	0.31	$0.2487 \pm 0.97849i$
0.50	0.38	$0.2484 \pm 0.9795i$
0.42	0.42	$0.2486 \pm 0.9740i$

Table 2

β_1	β_{2L}	λ
1.00	0.07	$-0.5570 \pm 0.84347i$
0.75	0.09	$-0.5507 \pm 0.8442i$
0.50	0.11	$-0.5510 \pm 0.8440i$
0.29	0.29	$-0.5407 \pm 0.8462i$

Hence, whenever $\beta_1 > \beta_L$ (β_1 fixed) the threshold β_{2L} is smaller than the “old” threshold β_L . On the other hand, the locations of the eigenvalues at bifurcation threshold are almost identical. Thus, on the whole, whenever $\beta_2 < \beta_{2L}$ the dynamics must be qualitative similar to what was found in Case 1 and Case 2, the main difference is the “speed” in which stability is achieved. Biologically, this makes sense. If β_1 is large, then the predator has great impact on the prey also at small predator densities, hence one should expect a faster reduction of the size of the prey population which again indicates that stability is gained at a lower threshold.

If we continue to increase β_2 above the threshold β_{2L} (keeping β_1 fixed) the only dynamics found is the stable fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$, we do not find a second Hopf bifurcation threshold β_{2H} . However, from a biological point of view, it is an open question if it makes sense to consider $\beta_2 > \beta_1$ (although we have discussed β_1 and β_2 not in terms of any units, $\beta_2 > \beta_1$ suggests that in this part of parameter space, the predator gains more from the prey than the prey is able to offer), so in the following we shall deal with the case $\beta = \beta_1 = \beta_2$ exclusively.

Let us now turn to the dynamics and the role of the predator in case of β small. In all the cases discussed in the previous section we found that an increase of the coupling parameter acts as a stabilizing effect. In fact, it is tempting to conjecture that an increase

of β (β small) in the “prey–predator” maps (15), (21), (34), (41), (48) acts qualitatively more or less in the same way as a decrease of the fecundity F in the “prey” maps (14), (22), (23) and (36). In order to support such a conjecture one has to show that the eigenvalues of the linearized “prey–predator” maps cross the unit circle (roughly!) at the same place as the eigenvalues of the linearized “prey” maps.

Now, at bifurcation threshold $F_1 = [1/(1 + \sigma P)] \exp[(1 + 2\sigma P)/(1 + \sigma P)]$, ($F_2 = \sigma F_1$), the eigenvalues of the linearized map of (14) may be written as

$$\lambda = \frac{1}{2(1 + \sigma P)} \left[1 \pm \sqrt{4(1 + \sigma P)^2 - 1} i \right] \quad (57)$$

and in Table 3 we show some numerical values of the eigenvalues at bifurcation threshold of the linearized map of (15) in case of $P = 0.6$ and clearly, the eigenvalues shown in Table 3 and the values of (57) in the cases $P = 0.6$, $\sigma = 1, 5/3, 2$ are very close.

Table 3

$F_1 = 4$	$\sigma = 1$	$G_1 = G_2 = 5$	$Q = 0.5$	$\beta = 0.26$	$\lambda = 0.294 \pm 0.958i$
$F_1 = 3$	$\sigma = \frac{5}{3}$	$G_1 = G_2 = 2$	$Q = 0.9$	$\beta = 0.42$	$\lambda = 0.249 \pm 0.974i$
$F_1 = 3$	$\sigma = 2$	$G_1 = 3, G_2 = 4$	$Q = 0.7$	$\beta = 0.29$	$\lambda = 0.221 \pm 0.977i$

Similar conclusions may be obtained by comparing the “prey” maps (22) and (38) with the corresponding “prey–predator” maps (21) and (41). For example: The eigenvalues of the linearized map of (22) at bifurcation threshold are

$$\lambda = -\frac{1}{2P} \pm \frac{1}{2P} \sqrt{4P^2 - 1} i \quad (58)$$

$\approx -0.555 \pm 0.831i$ in the special case $P = 0.9$, and as mentioned the modulus 1 solution of (30) at bifurcation threshold $\beta_L = 0.29$ is $\lambda = -0.541 \pm 0.846i$. Hence, our conjecture is supported.

Let us now turn to the question of periodicity. In the “prey” maps (22), (36) and (38) we found several examples of periodic dynamics of low period (either exact or approximate) in large parameter regions, the chaotic regime included. (In consideration of (36); if $\gamma \rightarrow -\alpha_1 F_2 / 2(\alpha_1 F_2 + \alpha_2)$ (cf. Theorem 3), the 4-periodicity is even more pronounced than in the case $\gamma \rightarrow 0$ which was discussed in Case 4, cf. Wikan (1997).)

One of the most significant results obtained from the previous section was that the inclusion of the predator does not seem to be capable of altering the periodicity of the prey as long as both species are in the unstable parameter region $\beta < \beta_L$. In fact, what we find is that the prey periodicity is reflected in similar cycles of the predator, a result which seems to be unaffected by the type of functions we use in the description of the predator. It is interesting to notice that such phenomena have indeed been observed in nature, especially among vole and lemming species, cf. Stenseth and Ims (1993) and references therein.

Another aspect which also should be mentioned is that the growth of the prey (not the predator!) is low during the low phase of the cycle, cf. Figure 10. It is an open question what prevents population growth during the low phase, see Boonstra et al. (1998). A comparison between 4-cycles generated by the “prey” map (38) and 4-cycles generated by the “prey–predator” map (41) (cf. Figure 9), indicates that the predator to a certain extent may damp the growth of the prey during the low phase, but the effect seems to be too small in order to explain why the growth is so low as observed.

Finally, let us turn to the dynamics and the role of the predator in case of β large. Except for the last map (map (50)) under Case 4, one of our main findings from Section 3 was that there exists a value $\beta_S \in [\beta_L, \beta_H]$ such that an increase of β beyond β_S acts as a destabilizing effect. All the maps also share the common feature that their unique nontrivial fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ undergoes a (supercritical) Hopf bifurcation at the threshold β_H . Hence, for $\beta > \beta_H$, $|\beta - \beta_H|$ small, the dynamics is restricted on an invariant curve. We have verified through simulations that the last result remains valid also in cases where we adjust the prey parameter F_1 , F_2 and P such that the prey possesses a stable fixed point in absence of the predator, cf. Theorem 1, 2 and 3.

When β ($\beta > \beta_H$) is further increased the populations reenter the chaotic regime. On the route to chaos (which may differ from case to case, although the Curry and Yorke route seems to be the most common, see Caswell (1989)), we have found a few examples of periodic dynamics (Case 4) but in contrast to $\beta < \beta_L$ the period this time is large, typically 12 or 14. The generic case is that there is no periodicity.

Appendix A

Proof of Theorem 2 in the main text

Using the abbreviation $f = F(1 - \gamma x)^{1/\gamma}$ (evaluated at equilibrium!) the eigenvalue equation of the linearized map may be written as

$$\lambda^2 - (f'x^* + f)\lambda - P(f'x^* + f) = 0 \quad (\text{A1})$$

and by use of the Jury criteria

$$1 - a_1 + a_2 > 0 \quad (\text{A2})$$

$$1 - |a_2| > 0 \quad (\text{A3})$$

cf. Murray (1993), where $a_1 = -(f'x^* + f)$ and $a_2 = -P(f'x^* + f)$, it is straightforward to show that the flip governs the dynamics whenever $0 < P < \frac{1}{2}$ and that the corresponding Hopf interval is $\frac{1}{2} < P < 1$. Further the critical parameter values in the flip and Hopf cases respectively are easily found to be

$$F_F = \frac{1}{1+P} \left[1 + \gamma \frac{2}{1-P} \right]^{1/\gamma} \quad F_H = \frac{1}{1+P} \left[1 + \gamma \frac{1+2P}{P} \right]^{1/\gamma} \quad (\text{A4})$$

So what remains to prove is that the bifurcations are of the supercritical type.

(A) Define the matrix

$$T = \begin{pmatrix} -\frac{1}{P} & -\frac{1}{1-P} \\ 1 & 1 \end{pmatrix}$$

which columns are the eigenvectors corresponding to the real eigenvalues of (A1) in the flip case.

Then, after expanding the first component of the map (23) up to third order, applying the change of coordinates $(\hat{x}_1, \hat{x}_2) = (x_1 - x_1^*, x_2 - x_2^*)$ in order to transform the bifurcation to the origin, together with the transformations

$$\begin{pmatrix} \hat{x}_1 \\ \hat{x}_2 \end{pmatrix} = T \begin{pmatrix} u \\ v \end{pmatrix} \quad \begin{pmatrix} u \\ v \end{pmatrix} = T^{-1} \begin{pmatrix} \hat{x}_1 \\ \hat{x}_2 \end{pmatrix}$$

the map may be cast into standard form as

$$(u, v) \rightarrow \left(-u + g(u, v), -\frac{P}{1-P}v - g(u, v) \right) \quad (\text{A5})$$

where

$$g = A [(1-P)^2u + P^2v]^2 + B [(1-P)^2u + P^2v]^3$$

and

$$A = \frac{1}{P(2P-1)(1-P)} \{1\} \quad B = -\frac{1}{P^2(2P-1)(1-P)^2} \{2\}$$

and

$$\{1\} = f' + \frac{1}{2} f'' x^* \quad \{2\} = \frac{1}{2} f'' + \frac{1}{6} f''' x^*$$

The next step involves the restriction of (A5) to the center manifold. To do this we first seek the center manifold as a graph

$$v = i(u) = Ku^2 + Lu^3 \quad (\text{A6})$$

and by inserting this expression into (A5) the center manifold (up to third order) may be found from the relation

$$i(-u + g(u, i(u))) + \frac{P}{1-P} i(u) + g(u, i(u)) = 0$$

from which we obtain

$$K = -(1-P)^5 A \quad L = (1-P)^7 [B + 2A^2(1-P)(1-2P)] \quad (\text{A7})$$

and finally by substituting (A6) (together with (A7)) into the first component of (A5) we obtain the restricted map

$$u \rightarrow p(u) = -u + A(1-P)^4 u^2 + (1-P)^6 [B - 2A^2 P^2 (1-P)] u^3 \quad (\text{A8})$$

Now according to theorem 3.5.1 in Guckenheimer and Holmes (1990) the bifurcation will be supercritical if the relations

$$\frac{\partial p}{\partial F} \frac{\partial^2 p}{\partial u^2} + 2 \frac{\partial^2 p}{\partial u \partial F} = \frac{\partial p}{\partial F} \frac{\partial^2 p}{\partial u^2} - \left(\frac{\partial p}{\partial u} - 1 \right) \frac{\partial^2 p}{\partial u \partial F} \neq 0 \quad (\text{A9})$$

$$\frac{1}{2} \left(\frac{\partial^2 p}{\partial u^2} \right)^2 + \frac{1}{3} \left(\frac{\partial^3 p}{\partial u^3} \right) > 0 \quad (\text{A10})$$

holds at the bifurcation.

To this end it is easy to show that the left hand side of the nongeneracy condition (A9) may be written as

$$-2 \left[\frac{2\gamma}{1-P} + 1 \right]^{1-(1/\gamma)} \frac{(1-P)^2}{1-2P}$$

which is clearly nonzero whenever $\gamma > -(1-P)/2$ and $0 < P < 1/2$. The left hand side of (A10) may be expressed as

$$\left[\frac{2\gamma}{1-P} + 1 \right]^2 \frac{2(1-P)^3}{P^2(1+P)(1-2P)} \left\{ (P-\gamma)^2 + \frac{1}{6}(1-\gamma)(4\gamma-3P+1) \right\}$$

and since $\gamma > -1/2$ ensures that $\gamma > -(1-P)/2$ holds for all P , $0 < P < 1/2$, the parenthesis $\{ \} > P^2 + (1/4)P > 0$. Hence, the left hand side of (A10) is positive and part (A) of Theorem 1 is proved.

(B) To prove part (B), that the Hopf is supercritical, we first argue along the same line as in (A) but the matrix T now consists of the real and imaginary parts of the eigenvectors as columns. Hence,

$$T = \begin{pmatrix} -\frac{1}{2P^2} & -\frac{b}{2P^2} \\ 1 & 0 \end{pmatrix}$$

where $b = \sqrt{4P^2 - 1}$. The corresponding map to (A5) now becomes

$$\begin{pmatrix} u \\ v \end{pmatrix} \rightarrow \begin{pmatrix} -\frac{1}{2P} & -\frac{b}{2P} \\ \frac{b}{2P} & -\frac{1}{2P} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} 0 \\ g(u, v) \end{pmatrix} \quad (\text{A11})$$

where

$$g(u, v) = A [(2P^2 - 1)u - bv]^2 + B [(2P^2 - 1)u - bv]^3$$

and

$$A = -\frac{1}{2bP^2}\{1\} \quad B = -\frac{1}{4bP^4}\{2\}$$

where $\{1\}$ and $\{2\}$ are defined through formulae (A5).

Following Guckenheimer and Holmes (1990) (theorem 3.5.2), the bifurcation is of the supercritical type if

$$\frac{d}{dF} |\lambda| > 0 \quad (\text{A12})$$

at bifurcation (which ensures that the eigenvalues leave the unit circle at bifurcation) and that the quantity

$$a = -\text{Re} \left[\frac{(1-2\lambda)\bar{\lambda}^2}{1-\lambda} \xi_{11}\xi_{20} \right] - \frac{1}{2} |\xi_{11}|^2 - |\xi_{02}|^2 + \text{Re}(\bar{\lambda}\xi_{21}) \quad (\text{A13})$$

is negative at the bifurcation. Here

$$\begin{aligned} \xi_{20} &= \frac{1}{8} [2g_{uv} + i(g_{uu} - g_{vv})] \\ \xi_{11} &= \frac{1}{4} i [g_{uu} + g_{vv}] \\ \xi_{02} &= \frac{1}{8} [-2g_{uv} + i(g_{uu} - g_{vv})] \end{aligned}$$

and

$$\xi_{21} = \frac{1}{16} [g_{uuv} + g_{vvv} + i(g_{uuu} + g_{uvv})]$$

Now, at our bifurcation

$$\frac{d}{dF} |\lambda| = \frac{P}{2} \left[1 + \gamma \frac{1+2P}{P} \right]^{(\gamma-1)/\gamma}$$

which is clearly positive.

Further

$$a = -\frac{1}{16(2P+1)(1+P)^2} \left[1 + \gamma \frac{1+2P}{P} \right]^2 h(\gamma)$$

where

$$h(\gamma) = (3P+2)[1-\gamma(1+2P)]^2 + (2P+1)(1+P)(1-\gamma)[P-1+2\gamma(1+2P)]$$

To complete the proof we must show that $h(\gamma) > 0$ whenever $1/2 < P < 1$.

$$h\left(-\frac{P}{1+2P}\right) = h_1 = (1+P)^2 > 0 \quad h(0) = h_2 = 2P^3 + P^2 + P - 1 > 0$$

and clearly $h_1 > h_2$.

Further

$$h'(\gamma) = (1 + 2P) [-P^2 - 6P - 1 + (12P^2 + 14P)\gamma] < 0$$

Hence, $h > 0$ and consequently $a < 0$.

Appendix B

Proof of Theorem 1 in the main text

The proof of Theorem 1 follows the same pattern as the proof of part (B) of Theorem 2 (cf. Appendix A). By applying the Jury criteria on the eigenvalue equation

$$\lambda^2 - \frac{1}{1 + \sigma P} \lambda + F_1^\gamma (1 + \sigma P)^\gamma x_2^* - \frac{\sigma P}{1 + \sigma P} = 0 \quad (\text{B1})$$

it is straightforward to show that the Hopf instability threshold is given by (11) in the main text. The “standard form” of (9) (cf. (A11)) now becomes

$$\begin{pmatrix} u \\ v \end{pmatrix} \rightarrow \begin{pmatrix} \frac{1}{2(1+\sigma P)} & -\frac{b}{2(1+\sigma P)} \\ \frac{b}{2(1+\sigma P)} & \frac{1}{2(1+\sigma P)} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} 0 \\ g(u, v) \end{pmatrix} \quad (\text{B2})$$

where

$$b = \sqrt{4(1 + \sigma P)^2 - 1}$$

$$g(u, v) = Au^2 + f'uv + Bu^3 + \frac{1}{2}f''u^2v$$

$$A = -\frac{1}{b} [f' + 2P(1 + \sigma P)\{1\}] \quad B = -\frac{1}{b} \left[\frac{1}{2}f'' + 2P(1 + \sigma P)\{2\} \right]$$

$$\{1\} = \sigma f' + \frac{1}{2}f'' \frac{1 + \sigma P}{P} x_2^* \quad \{2\} = \frac{1}{2}\sigma f'' + \frac{1}{6}f''' \frac{1 + \sigma P}{P} x_2^*$$

and f', f'', \dots are the derivatives of $f(x_2) = F_1(1 - \gamma x_2)^{1/\gamma}$ evaluated at equilibrium.

Now, the Hopf bifurcation is of the supercritical type whenever

$$\frac{d}{dF_1} |\lambda| > 0 \quad (\text{B3})$$

at bifurcation and that the “stability coefficient” a defined through (A13) is negative at bifurcation. For the problem at hand, (12) and (B1) gives

$$\frac{d}{dF_1} |\lambda| = \frac{1}{2} (1 + \sigma P) \left[1 + \gamma \frac{1 + 2\sigma P}{1 + \sigma P} \right]^{1-(1/\gamma)} > 0$$

and, using the abbreviation $w = 1 + \gamma(1 + 2\sigma P)/(1 + \sigma P) > 0$, a may be expressed as

$$a = V + Z \quad (\text{B4})$$

where

$$V = \frac{Aw}{64b(1 + \sigma P)^3} \{ [b^2(4 + \sigma P) - 3\sigma P] + \gamma(1 + \sigma P) [(3 + 6\sigma P)(1 - b^2) - 2b^2] \}$$

and

$$Z = -\frac{w^2}{16b^2(1 + \sigma P)^2} \{ b^2 + b^2(1 - \gamma) [\sigma^2 P^2 + 2\gamma(1 + \sigma P)^2] + 3[\sigma P - \gamma(1 + \sigma P)(1 + 2\sigma P)]^2 \}$$

Here we may notice that $V < 0$ since the parenthesis $\{ \}$ in V is positive ($b^2 > 3$) and

$$A = -\frac{1}{b(1 + \sigma P)} w [\sigma P - \gamma(1 + \sigma P)(1 + 2\sigma P)] < 0$$

Z is negative unless γ is close to -1 but in this case $|V| \gg |Z|$, thus $a = V + Z$ is negative also here, hence $a < 0$ everywhere and we conclude that the bifurcation is supercritical.

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References

- Bergh O. (1988) Stability of discrete age-structured and aggregated delay-difference population models.
Getz W. M. *J. Math. Biol.* **26**, 551–581
- Boonstra R. (1998) Population cycles in small mammals: The problem of explaining the low phase.
Krebs C. J. *Ecology* **79**(5), 1479–1488
Stenseth N. C.
- Caswell H. (1989) *Matrix Population Models*. Sunderland: Sinauer
- Costantino R. F. (1997) Chaotic dynamics in an insect population.
Desharnais R. A. *Science* **275**, 389–391
Cushing J. M.
Dennis B.
- Crowe K. M. (1994) A nonlinear ergodic theorem for discrete systems.
J. Math. Biol. **32**, 179–191
- Cushing J. M. (1988) Nonlinear matrix models and population dynamics.
Nat. Resour. Model **2**, 539–580
- Cushing J. M. (1989) A strong ergodic theorem for some nonlinear matrix models for the dynamics of structured populations.
Nat. Resour. Model **3**, 331–356
- Cushing J. M. (1998) *An introduction to structured population dynamics*. SIAM, Philadelphia

- Cushing J. M. (1996) An interdisciplinary approach to understanding
Dennis B. nonlinear ecological dynamics.
Desharnais R. A. *Ecol. Model* **92**, 111-119
Costantino R. F.
- Dennis B. (1997) Transition in population dynamics: equilibria to
Desharnais R. A. periodic cycles to aperiodic cycles.
Cushing J. M. *J. Animal Ecology* **66**, 704-729
Costantino R. F.
- Cushing J. M. (1998) Nonlinear population dynamics: Models, Experiments
Costantino R. F. and Data.
Dennis B. *J. Theor. Biol.* **194**, 1-9
Desharnais R. A.
Henson S. M.
- DeAngelis D. L. (1980) Stability and return times of Leslie matrices with
Svoboda L. J. density-dependent survival; Applications of fish
Christensen S. W. populations.
Vaughan D. S. *Ecol. Model* **8**, 149-163
- Desharnais R. A. (1987) Stable demographic limit cycles in laboratory
Liu L. populations of *Tribolium Castaneum*.
J. Animal Ecology **56**, 885-906
- Guckenheimer J. (1977) The dynamics of density dependent population
Oster G. models.
Ipaktchi A. *J. Math. Biol.* **4**, 101-147

- Guckenheimer J. (1990) *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields*.
 Holmes P. Springer Verlag, Berlin, Heidelberg, New York, Tokyo
- Levin S. A. (1980) Analysis of an age-structured fishery model.
 Goodyear P. H. *J. Math. Biol.* **9**, 245–274
- Levin S. A. (1981) Age-structure and stability in multiple-age spawning populations. In: *Renewable Resource Managements*. (Vincent T. L. Skowronski J. M., eds.), Heidelberg: Springer-Verlag
- Liu L. (1987) Equilibrium and local stability in a logistic matrix
 Cohen J. E. model for age-structured populations.
J. Math. Biol. **25**, 73–88
- Murray J. D. (1993) *Mathematical Biology*.
 Springer Verlag, Berlin, Heidelberg, New York
- Silva J. A. (1993) Effects of delay, truncation and density dependence
 Hallam T. G. in reproduction schedules on stability of nonlinear
 Leslie matrix models.
J. Math. Biol. **31**, 367–395
- Stenseth N. C. (1993) Population dynamics of lemmings: temporal and
 Ims R. A. spatial variation.
The Biology of Lemmings, N C. Stenseth and

R. A. Ims, Eds., Academic Press, London

- Wikan A. (1995) Periodicity of 4 in age-structured population models
Mjølhus E. with density dependence.
J. Theor. Biol. **173**, 109–119
- Wikan A. (1996) Overcompensatory recruitment and generation delay
Mjølhus E. in discrete age-structured population models.
J. Math. Biol. **35**, 195–239
- Wikan A. (1997) Dynamic consequences of reproductive delay in Leslie
matrix models with nonlinear survival probabilities.
Math. Biosci. **146**, 37–62

Figure Captions

Figure 1. The dynamics of (14) beyond the bifurcation threshold. Parameter values: (a)

$$F_1 = 2.5, P = 0.6; \text{ (b) } F_1 = 5.0, P = 0.6.$$

Figure 2 Stable attractors of the map (15). Parameter values: $F_1 = 3, F_2 = 5, P = 0.6,$

$$G_1 = G_2 = 2, Q = 0.9. \text{ (a) } \beta = 0.40; \text{ (b) } \beta = 1, 32.$$

Figure 3. The bifurcation diagram generated by map (15).

Figure 4a. The strange attractor in the case $(P, F) = (0.90, 18.50)$.

Figure 4b. The predator in the chaotic regime. Each of the 3 branches are visited once every 3rd iteration. ($\beta = 0.08$).

Figure 5. An exact 3-periodic orbit. $\beta = 0.26$. (a) The prey. (b) The predator.

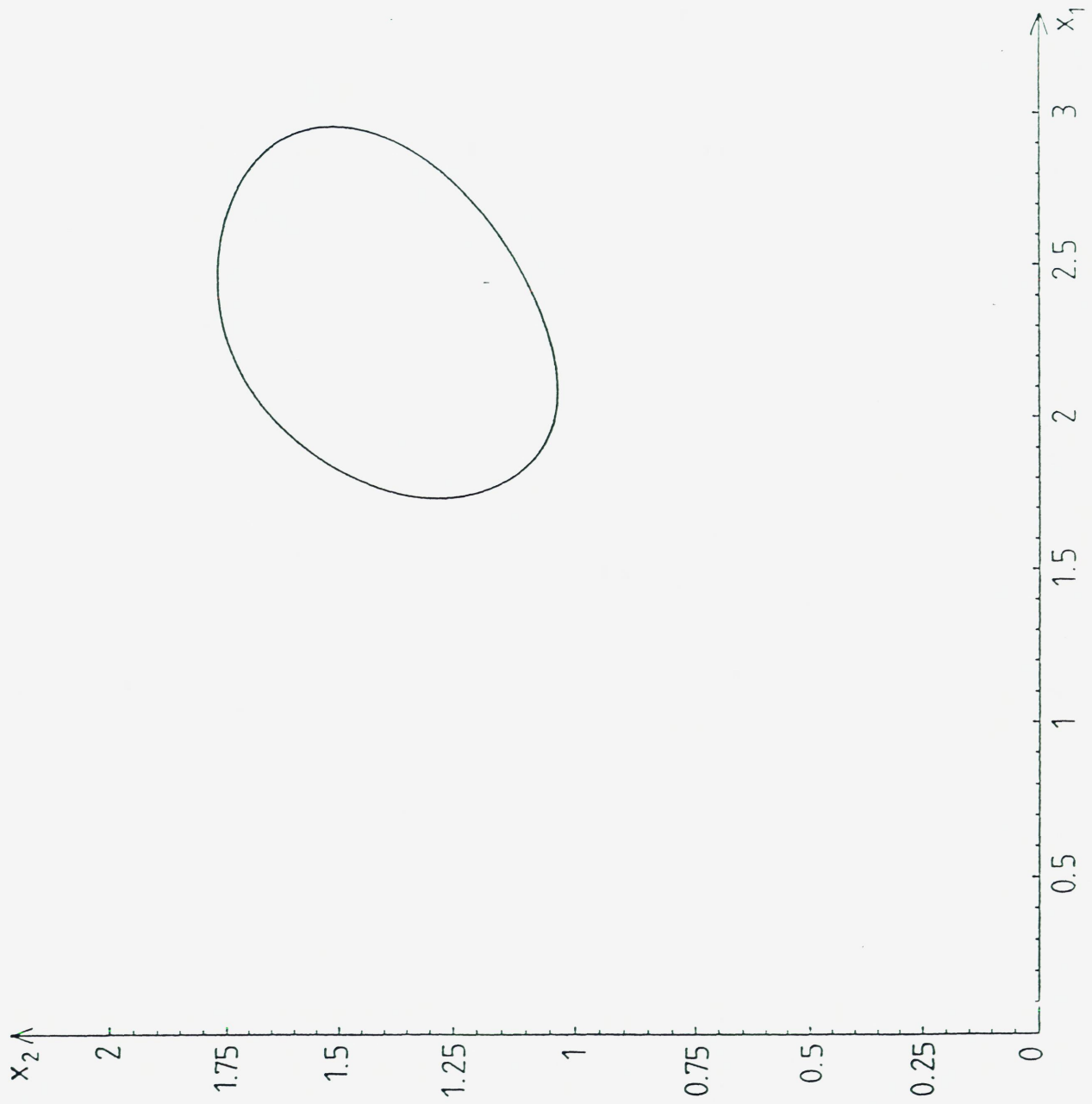
Figure 6. The prey dynamics beyond β_H , $|\beta - \beta_H|$ small.

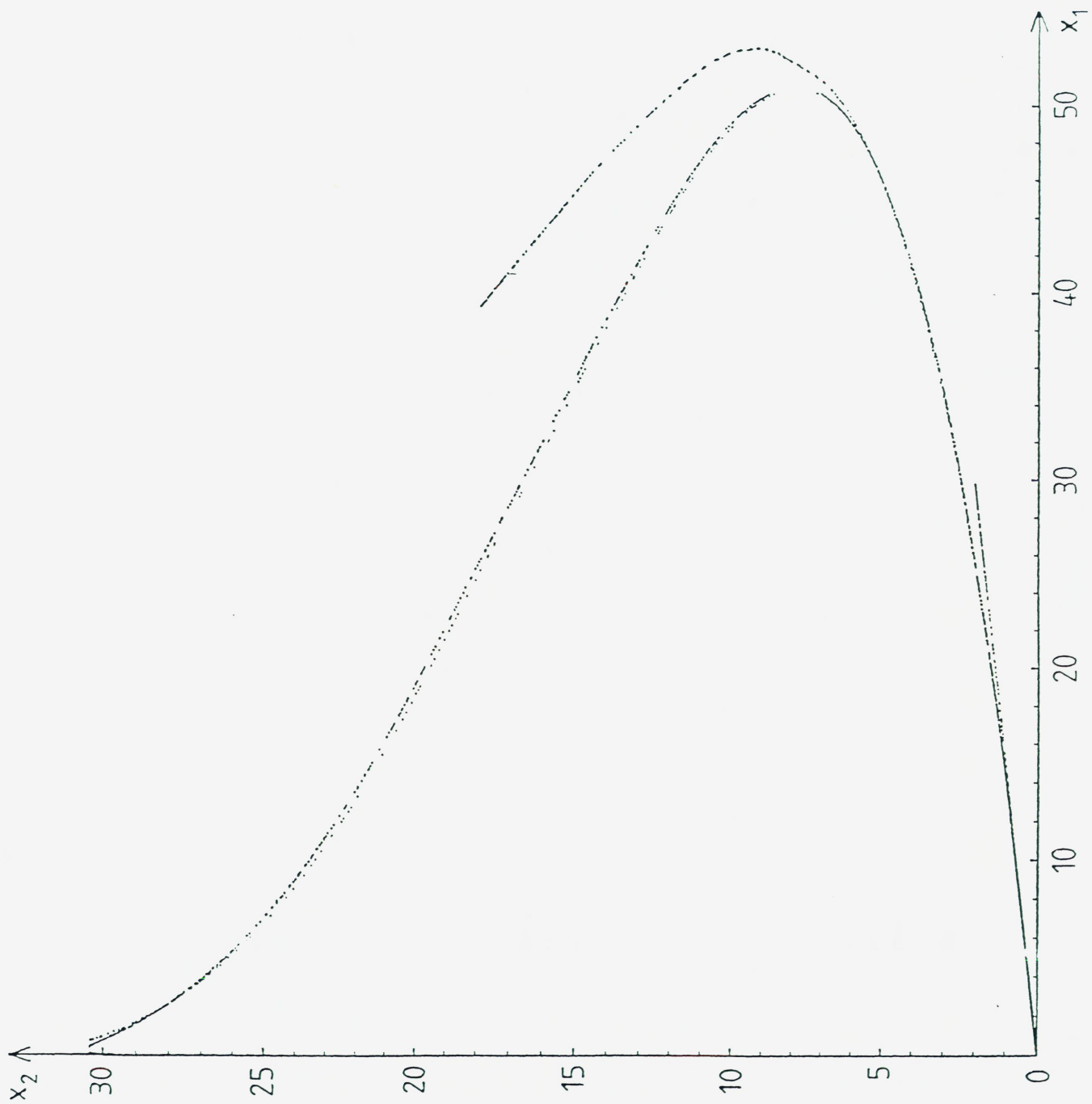
Figure 7. The bifurcation diagram generated by map (34).

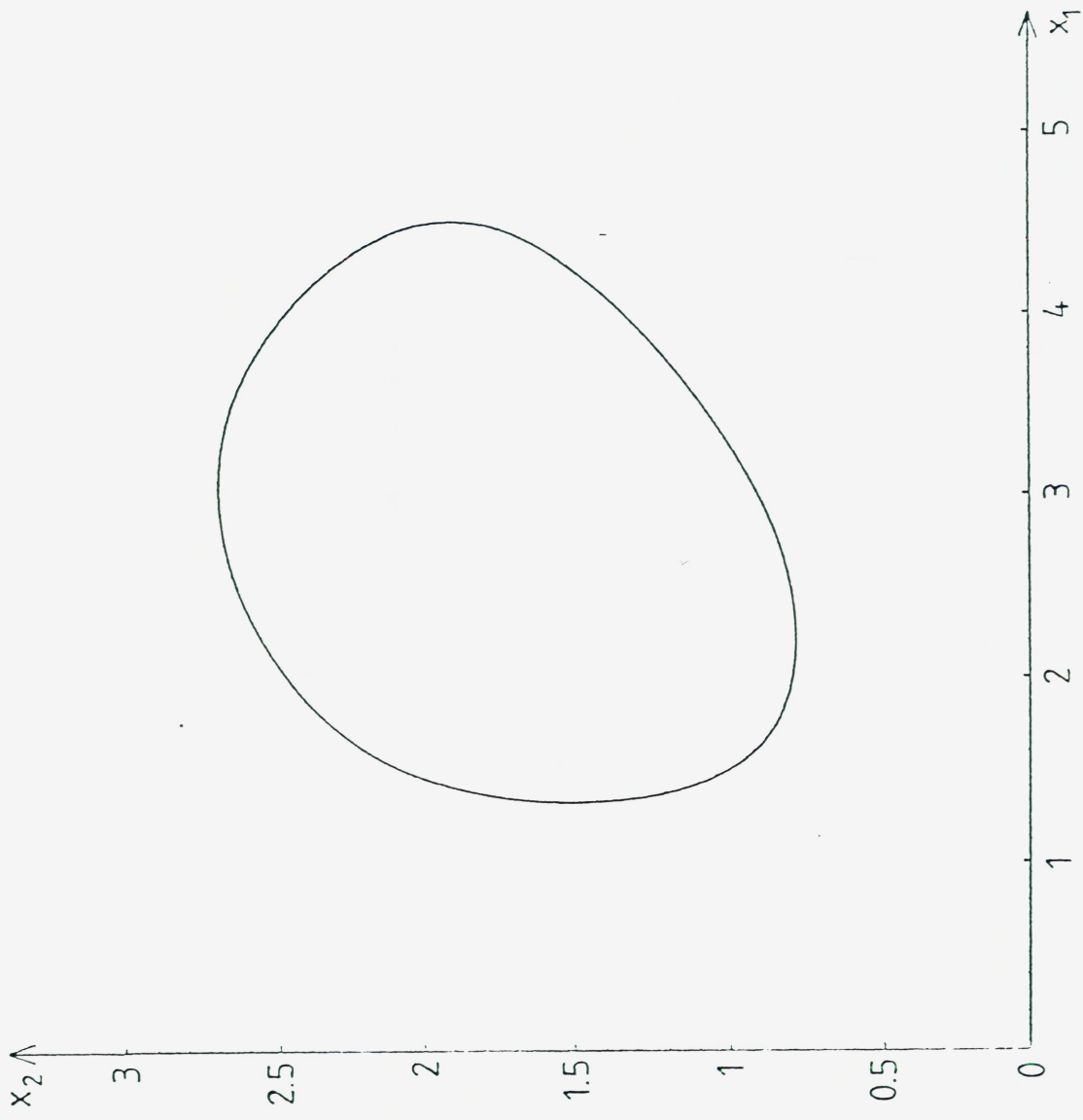
Figure 8. The map (38) in the chaotic regime. The strange attractor has been divided into 4 disjoint subsets which are visited once in each cycle. The dynamics goes clockwise. ($P = 0.6, F_2 = 25$).

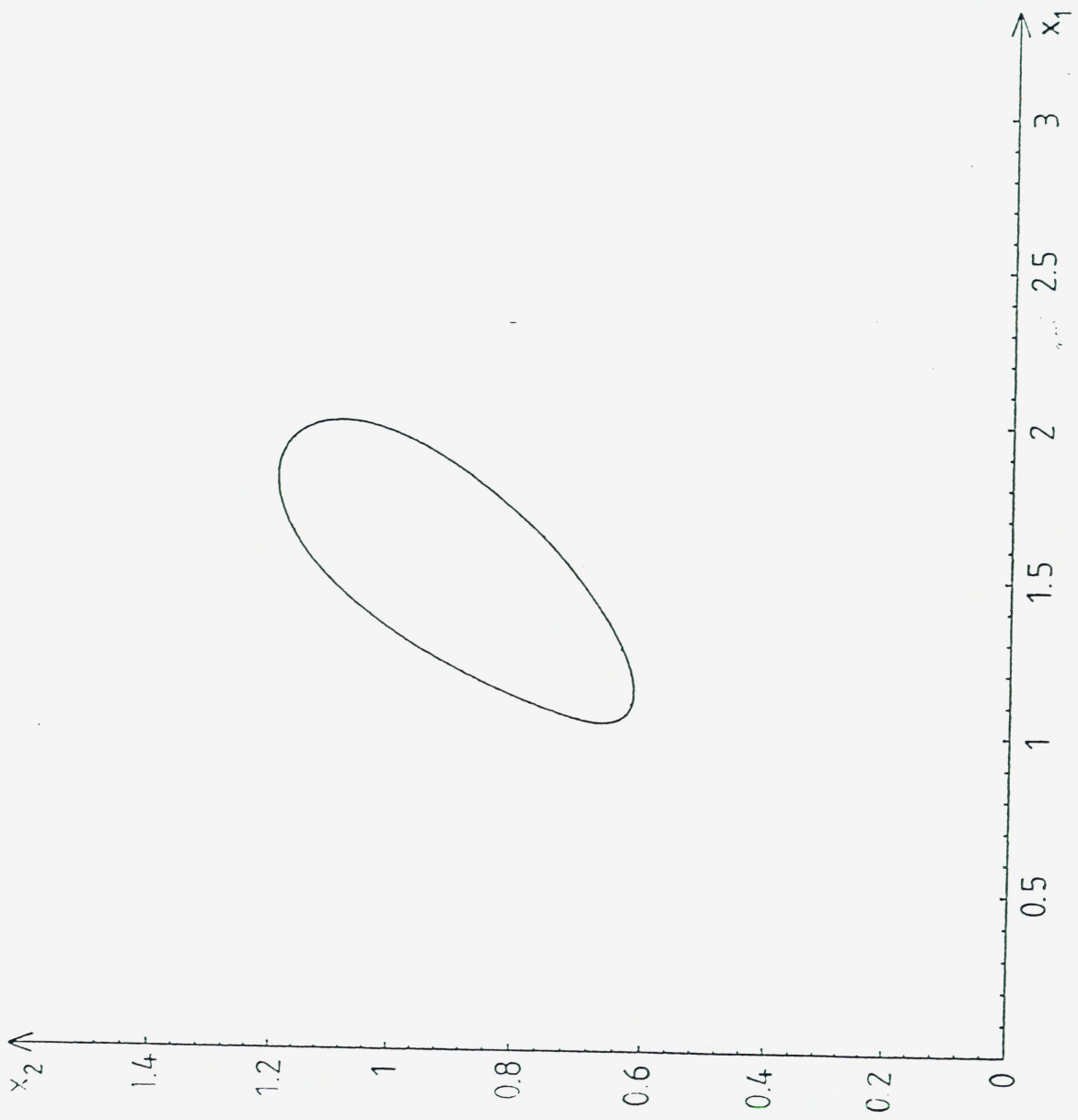
Figure 9. An exact 4-periodic orbit (map (41)). The “upper” orbit belongs to the prey, the “lower” to the predator. ($P = Q = 0.6, F_2 = 25, G_2 = 12, \beta = \beta_1 = \beta_2 = 0.20$).

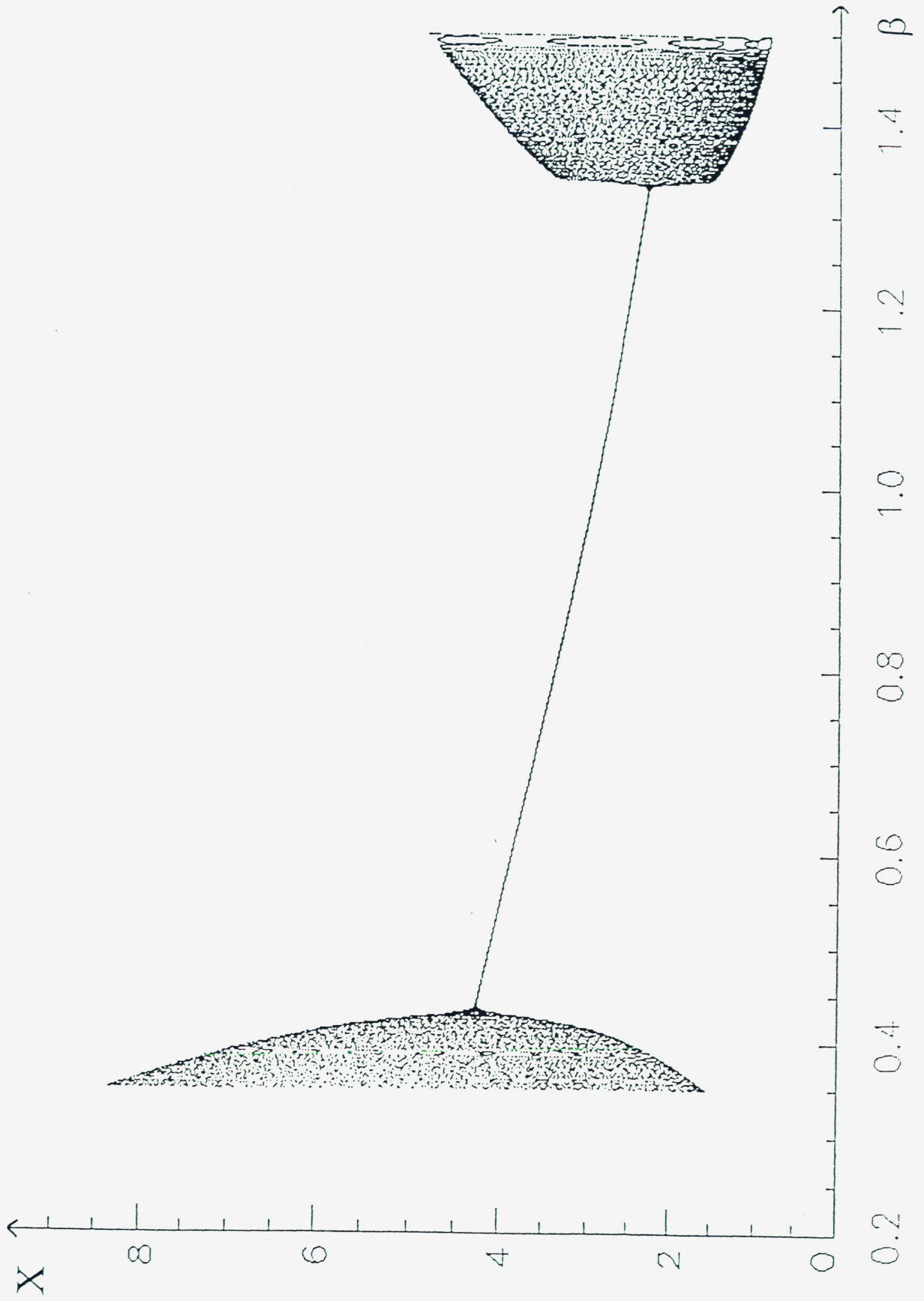
Figure 10. The bifurcation diagram generated by map (41).

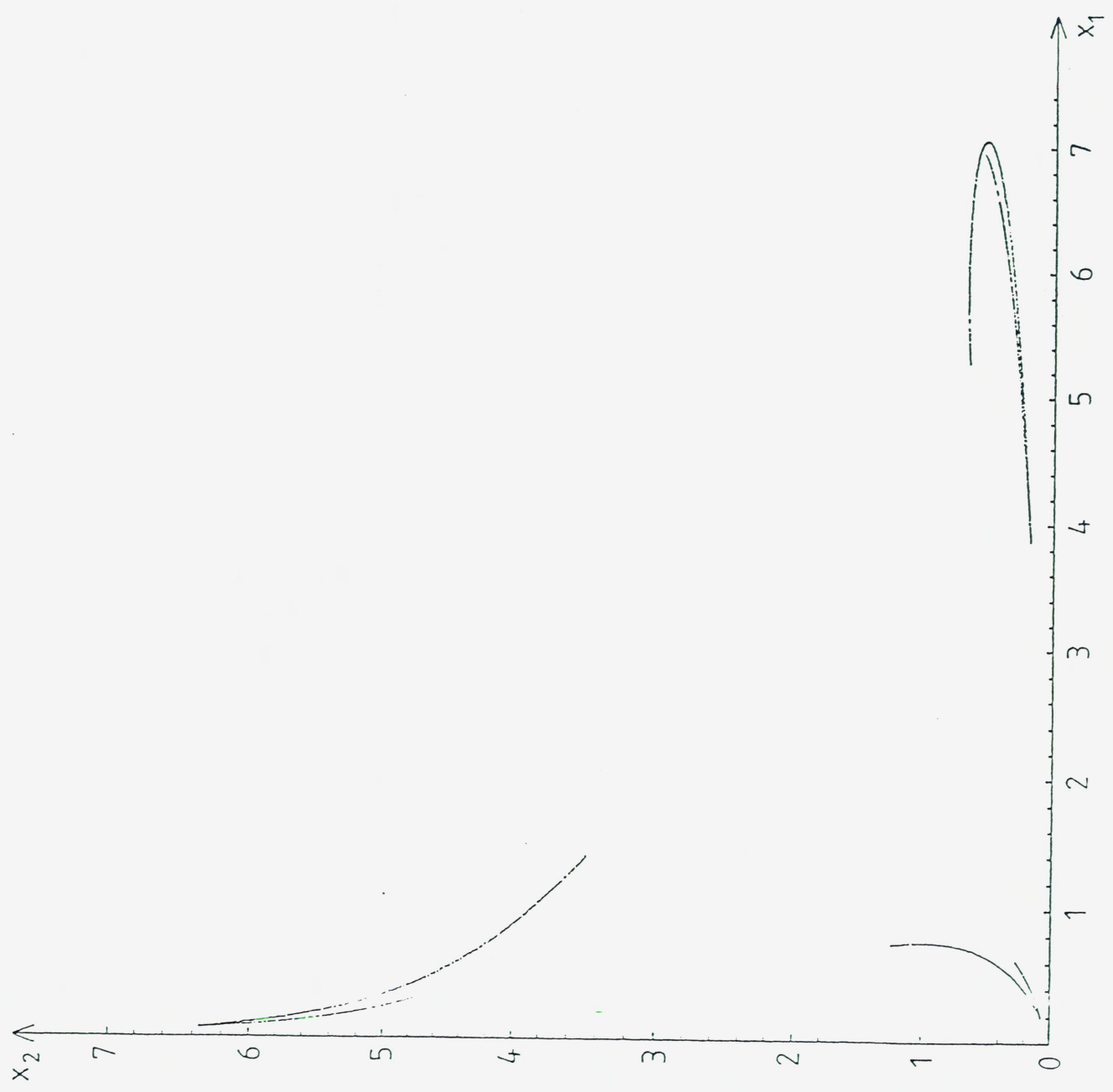


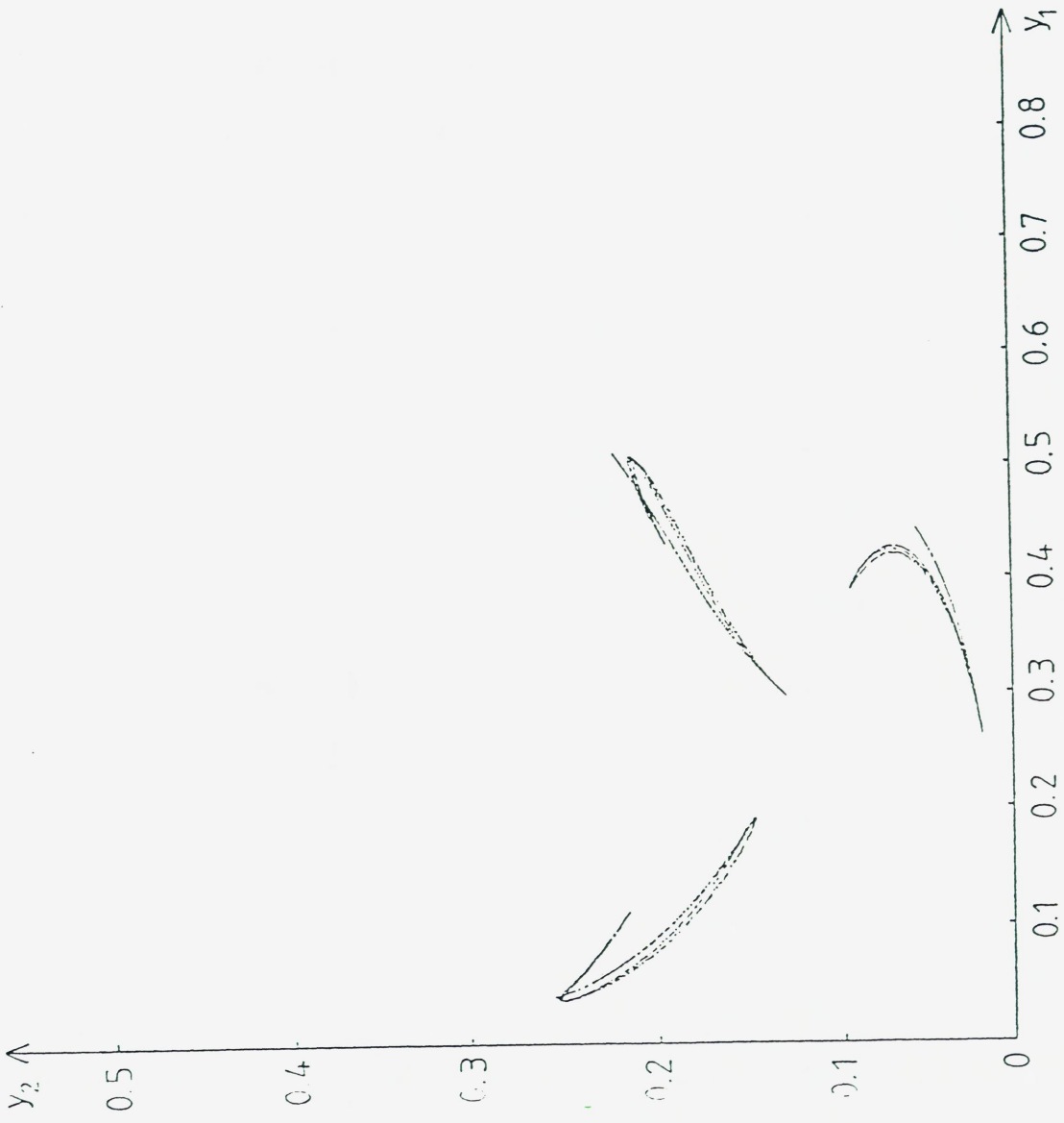


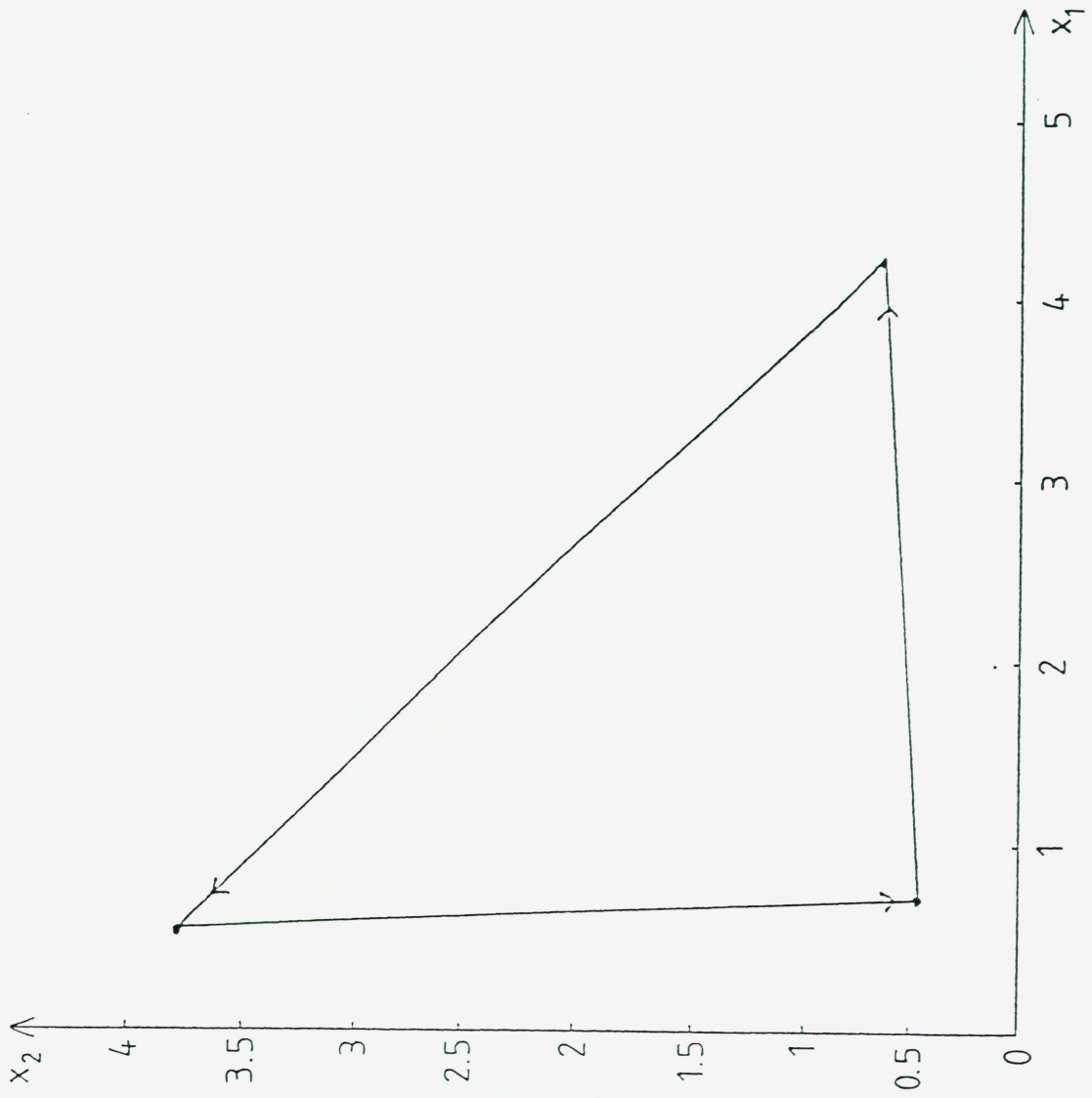


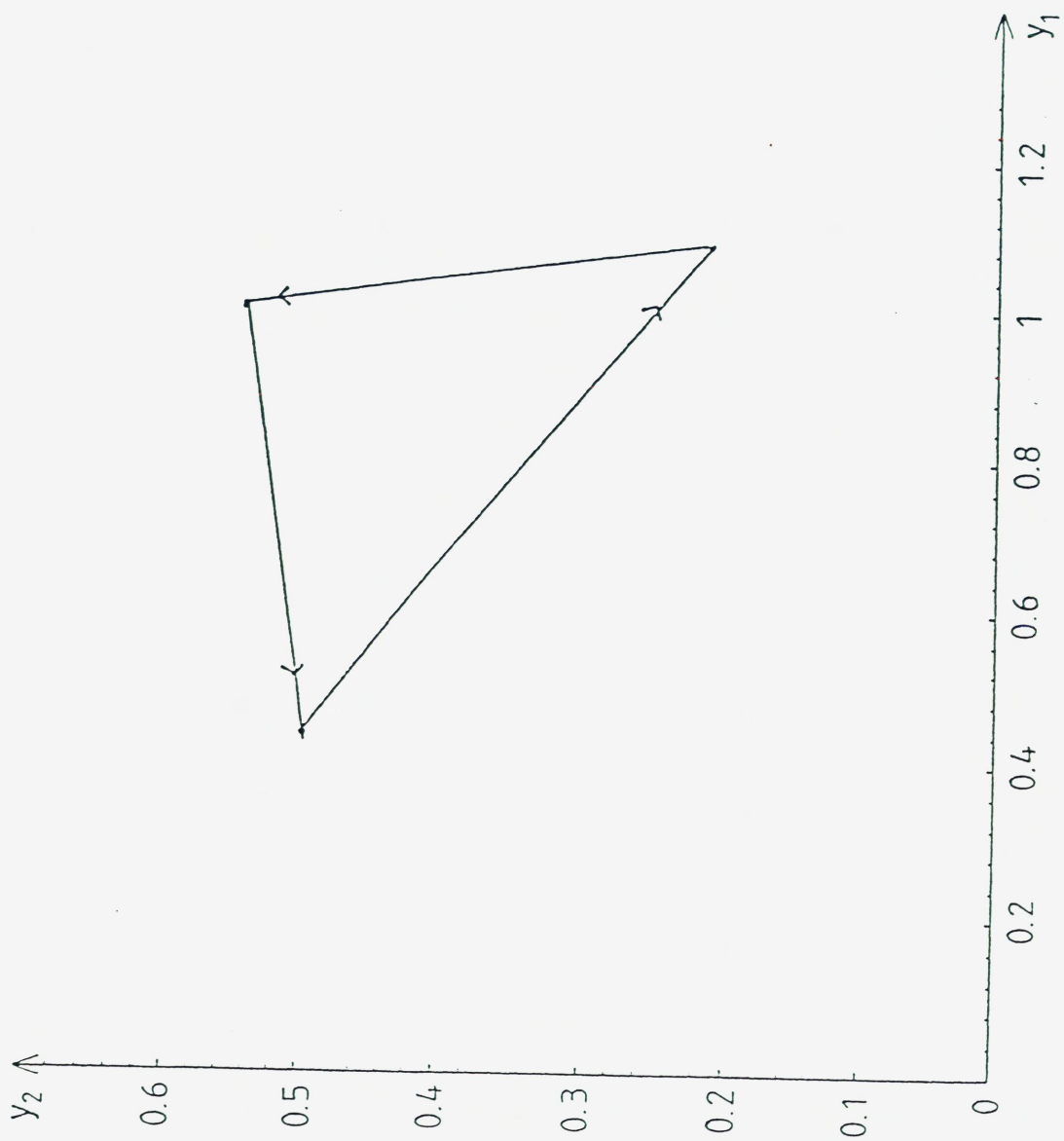


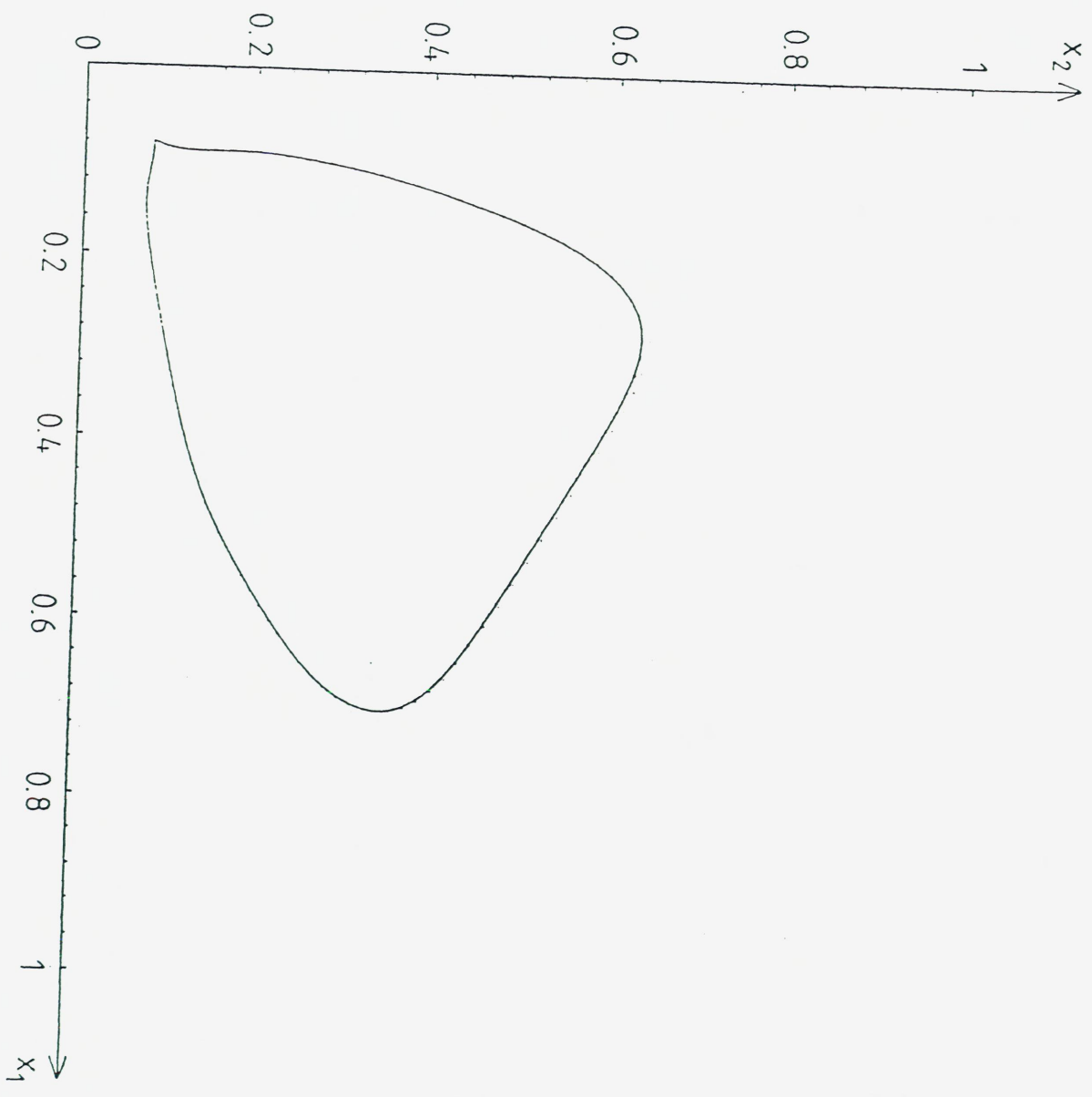




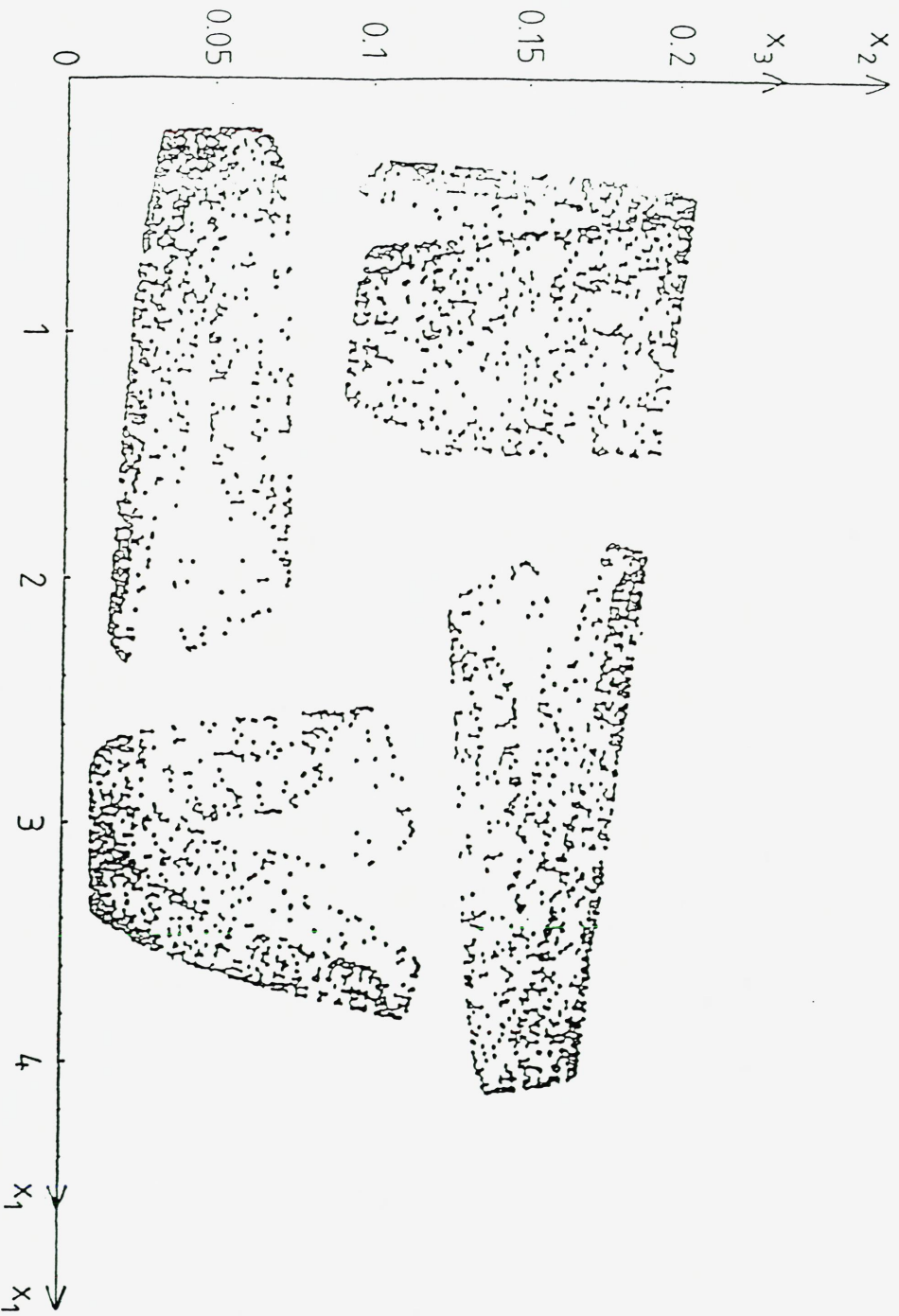


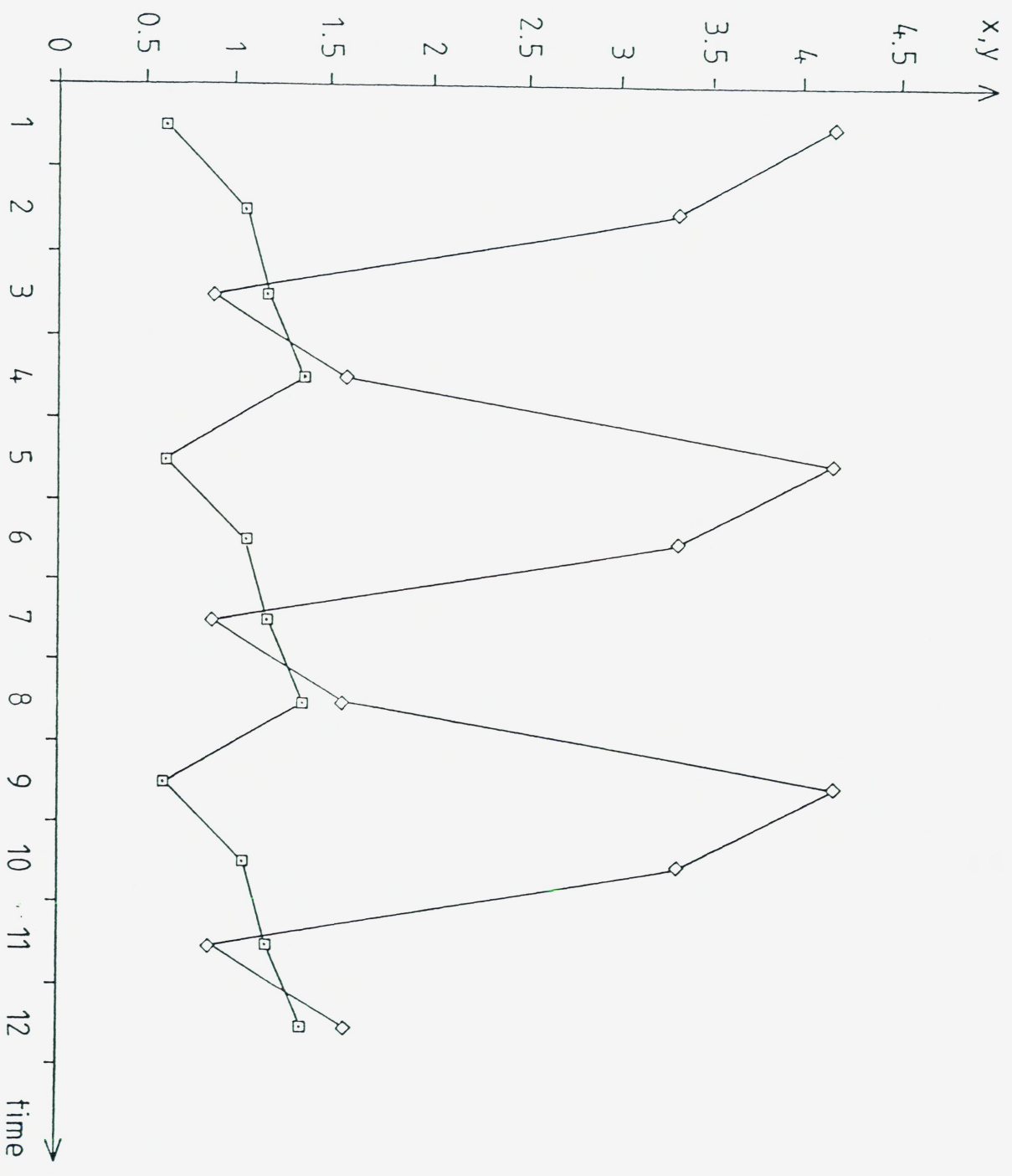


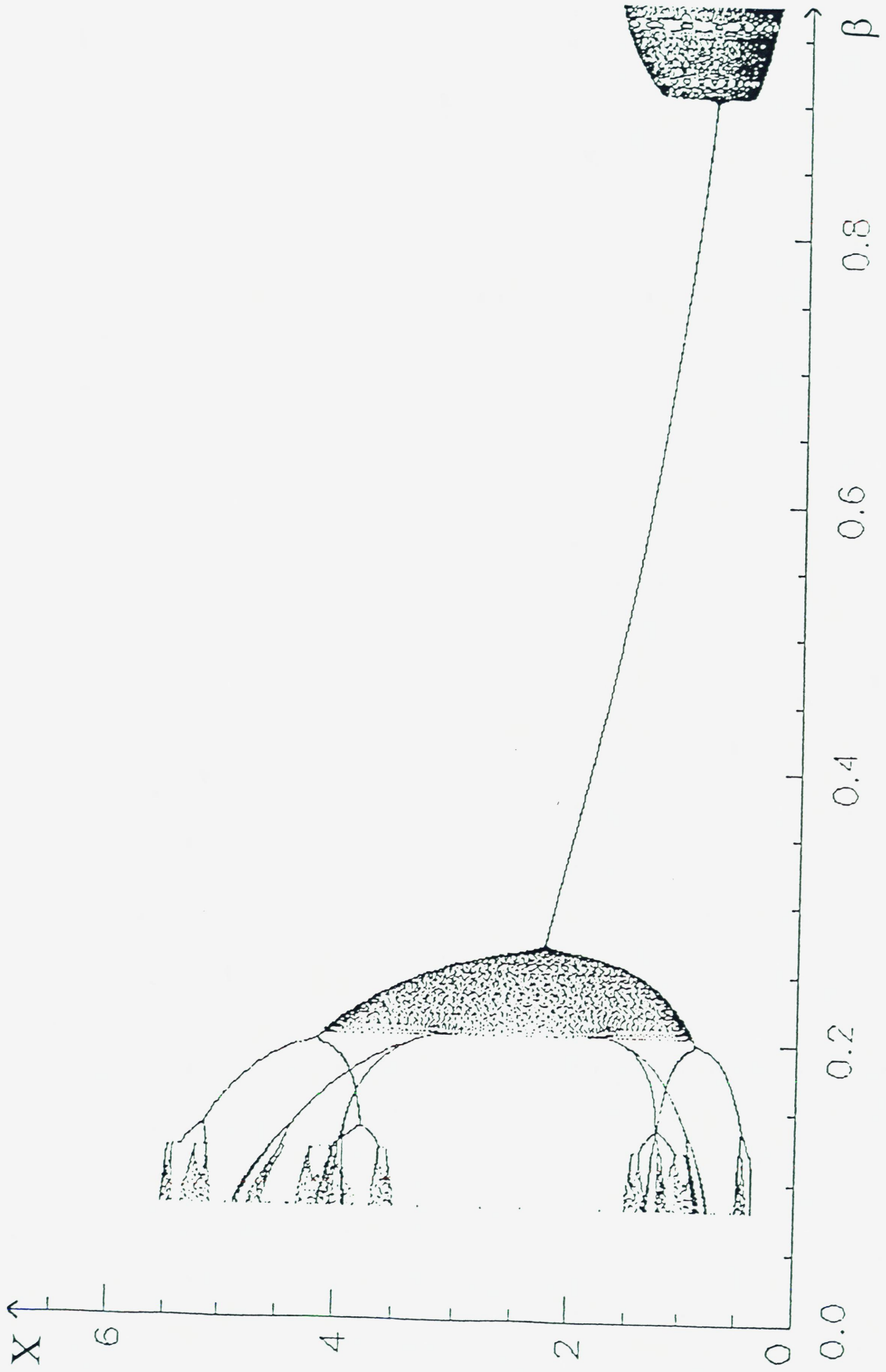














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