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An analysis of a stage-structured
population model

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Sammendrag/Abstract

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Our findings are compared with findings from other models and we propose that it is a fairly general ecological principle that iteroparous species are more stable than semelparous species.

Stikkord/ Key Words	Semelparity, Iteroparity, Stage-structure, Permanence, Stability	

Semelparity versus Iteroparity
An analysis of a stage-structured population model

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Abstract

A discrete two-stage structured population model is established and analysed. In one direction we state and prove a theorem which says that the model is permanent (i.e. that the population will neither go extinct nor exhibit explosive oscillations). In another direction we use the model in order to reveal and compare the possible dynamical properties of semelparous and iteroparous species and in doing so we include density dependence both in the recruitment and in the survival terms. We also analyse a similar semelparous age-structured model. Regarding the latter we prove that if the strength of density dependence is greater in the fecundity than in the survival term the nontrivial equilibrium of the model will never be stable. Instead the dynamics will converge towards a state where the whole population is in one age class. As we show, such dynamics may be chaotic. Considering the stage-structured model we compare our findings with the findings from other models and propose that it is a fairly general ecological principle that iteroparous species are more stable than semelparous species. We also give several examples of the dynamics in unstable and chaotic parameter regions.

Keywords: Semelparity, Iteroparity, Age-structure, Stage-structure, Bifurcation.

1. Introduction

A species is called semelparous if it reproduces only once during its lifetime. It is called iteroparous in case of repeatedly reproduction. Regarding fish populations, important commercial interesting species like the northeast arctic cod stock may be classified as an iteroparous species while most salmon species are semelparous. There are obvious reasons why it is important to understand the dynamical properties of such species. Among several alternatives, the use of nonlinear age-structured (matrix) models has proved to be a powerful tool when trying to reveal the dynamics both in fish and in other populations, cf. Cushing (1998) and Caswell (2001). Much of this work has been inspired by the seminal work of Ricker (1954) who studied the effects of age structure on a population with nonlinear recruitment. A summary of the most important of Ricker's findings may be obtained in Higgins *et al.* (1997). Relevant examples where age-structured matrix models have been applied on concrete species may be found in Cooke & Leon (1976), Longstaff (1977), Levin & Goodyear (1980), Hastings (1984), and Desharnais & Liu (1987). Lots of other examples are given in Caswell (2001). 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, cf. Guckenheimer *et al.* (1977), Silva & Hallam (1993), Wikan & Mjølhus (1995). In Wikan & Mjølhus (1996), Wikan (1997), Davydova *et al.* (2003) and Mjølhus *et al.* (2005) special attention is devoted to semelparous species and from the papers quoted above it is clear that the dynamical properties of semelparous species often are substantially different to what one finds in studies of the iteroparous

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case. For example, in semelparous species models one may have the phenomenon of synchronization, i.e. convergence to a dynamical state where the whole population is in one age class only. Such behaviour is not found in iteroparous species models.

The purpose of this paper is to establish and compare the possible dynamical outcomes of semelparous and iteroparous species models but in doing so we will use a stage-structured rather than an age-structured population model. In many respects the choice of model is motivated by Neubert & Caswell (2000) and Wikan & Eide (2004) but also from the fact that some species (both itero- and semelparous) may live several years before they reproduce while others become mature after a short time and for comparison reasons we find it more convenient to use a stage-structured model with two stages (mature and immature). Finally, it should also be mentioned that "small" stage- structured models are fully capable of describing and even predicting nonstationary and chaotic behaviour in populations, see Cushing *et al.* (1996), Costantino *et al.* (1997), Dennis *et al.* (1997) and Cushing *et al.* (1998).

The plan of the paper is as follows: In Section 2 we present and discuss the model. In Section 3 we analyse possible dynamical outcomes and finally, in Section 4 we summarize, unify and discuss our findings.

2. The model

Let $x_{1,t}$ and $x_{2,t}$ be the immature and the mature part of a population at time t respectively. We further assume that $f(x)$ is the fecundity (the number of juveniles produced by a mature individual) and that $p(x)$ is the fraction of the immature population

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that survives to become mature. $x = x_1 + x_2$, u_1 and u_2 are (natural) death rates and finally it is also assumed that the remaining part of the immature population $(1 - u_1)x_1$ is reduced by a nonlinear factor $s(x)$. Then the relation between x_1 and x_2 at two consecutive time steps (years) may be expressed as

$$x_{1,t+1} = (1 - u_1)s(x_t)x_{1,t} + f(x_t)x_{2,t}$$

$$x_{2,t+1} = p(x_t)x_{1,t} + (1 - u_2)x_{2,t}$$

(1)

(1) may be regarded as a generalization of the model in Wikan & Eide (2004) where the Northeast Arctic cod stock was considered. (1) has also similarities with the general stage-structured model presented in Neubert & Caswell (2000).

Adopting the classification strategy from the latter, model (1) covers several life histories. Indeed, if $u_2 \to 1$ the population is semelparous (i.e. is reproducing only once). If $0 < u_2 < 1$ the population is iteroparous (repeatedly reproduction). The subclass characterized by $u_2 \to 1$ and $u_1 \to 1$ is often referred to as precocious semelparity which covers the situation for many annual plants and insects with rapid development followed by only one reproduction. Delayed semelparity occurs whenever $u_2 \to 1$ and $0 < u_1 < 1$. Typical examples of such species are periodical cicadas, see Behncke (2000) and Davydova *et al.* (2003), and several salmon species that live for many years before they become mature and then reproduce only once. The iteroparous case may also be divided into two subclasses. The case $0 < u_2 < 1$ and $u_1 \to 1$ is classified as precocious iteroparity and covers several small mammals species which start to reproduce at a young age and may survive to reproduce for several years. From a dynamic point of view the most exciting example here is the lemming. The fourth and last subclass is delayed iteroparity characterized by

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$0 < u_2 < 1$ and $0 < u_1 < 1$ which covers species which may live long before maturity and then survive to reproduce for many years. Typical examples are humans and other large mammals.

In the following we shall assume that the density-dependent terms in (1) may be written as a product of a constant term and a nonlinear term. Thus

$$s(x) = S\hat{s}(x) \qquad f(x) = F\hat{f}(x) \qquad p(x) = P\hat{p}(x) \tag{2}$$

where $0 \leq S \leq 1$, $0 < P \leq 1$, $F > 0$, $0 \leq u_1, u_2 < 1$, $0 < \hat{s}(x), \hat{p}(x), \hat{f}(x) \leq 1$, $\hat{s}(0) = \hat{p}(0) = \hat{f}(0) = 1$. This is the same strategy as used by several authors, see for example the striped bass fishery model by Levin & Goodyear (1980) or the Tribolium model by Cushing *et al.* (1998), see also Caswell (2001). Hence, we rewrite (1) as

$$x_{1,t+1} = (1 - u_1)S\hat{s}(x_t)x_{1,t} + F\hat{f}(x_t)x_{2,t}$$

$$x_{2,t+1} = P\hat{p}(x_t)x_{1,t} + (1 - u_2)x_{2,t} \tag{3}$$

or in matrix form

$$\mathbf{x}_{t+1} = A_x \mathbf{x}_t \tag{4}$$

where $\mathbf{x} = (x_1, x_2)^T$ and

$$A_x = \begin{pmatrix} (1 - u_1)S\hat{s}(x) & F\hat{f}(x) \\ P\hat{p}(x) & 1 - u_2 \end{pmatrix} \tag{5}$$

A final but important restriction that we also have to impose is $(1 - u_1)S + P \leq 1$. Otherwise, the fraction of juveniles that survive to become adults plus the fraction that survive but remain juveniles may be larger than 1 even in the case of zero fecundity which of course is unacceptable from a biological point of view.

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As is well known, population survival is a key feature in ecological models and there exist several mathematical criteria of such survival (Freedman *et al.*, 1987; Cushing, 1998; Crowe 2001; Kon *et al.*, 2004). Here we shall use the concept permanence as a criterion of population survival.

Definition 1

Let $x_t = x_{1,t} + x_{2,t}$ be the total population at time t. Model (3) is said to be permanent if there exist $\delta > 0$ and $D > 0$ such that

$$\delta < \liminf_{t \to \infty} x_t \leq \limsup_{t \to \infty} x_t < D$$

—

Thus, if a population model is permanent, the total population density neither explodes nor goes to zero.

Note that the definition of permanence (which is the same as in Kon *et al.* (2004)) permits that one of the stage (or age) classes $x_{1,t}$ or $x_{2,t}$ may be zero at time t. Such dynamics may indeed occur, see Bulmer (1977), Wikan & Mjølhus (1996), Davydova *et al.* (2003) and Mjølhus *et al.* (2005).

Define the inherent net reproductive number R_0 as

$$R_0 = \frac{PF}{u_2[1 - (1 - u_1)S]} \tag{6}$$

Then we have the following result regarding (3):

Theorem 1

Suppose that model (3) is continuous and that one of $\hat{p}(x)x_1$ or $\hat{f}(x)x_2$ is bounded from above. Further, assume that the matrix A_0 (see (5)) is irreducible and $\mathbb{R}_+^2 \setminus \{0\}$ forward invariant (i.e. that $A_x \mathbf{x} \in \mathbb{R}_+^2 \setminus \{0\}$ for all $\mathbf{x} \in \mathbb{R}_+^2 \setminus \{0\}$). Then model (3) is permanent provided $R_0 > 1$.

Proof

Cf. the Appendix.

As is shown in the proof of Theorem 1, the condition $R_0 > 1$ implies that the origin, which obviously is a fixed point of (3), is a repellor. Otherwise, the model would not be permanent so in the rest of the paper it is assumed that $R_0 > 1$.

If we in addition neglect Allé effects and suppose that $\hat{p}$, $\hat{s}$ and $\hat{f}$ are decreasing functions of x, (3) has also a unique nontrivial fixed point (x_1^*, x_2^*). Indeed, at equilibrium

$$(1 - u_1)s(x) + \frac{1}{u_2} f(x)p(x) = 1 \tag{7}$$

and here we may observe the following: When $x \to 0$ the left-hand side of (7) approaches

$$1 + (R_0 - 1)[1 - (1 - u_1)S]$$

which clearly is larger than unity. On the other hand, in case of large values of x, the left-hand side of (7) will become close to zero, hence there must exist an intermediate value x^* $(x^* = x_1^* + x_2^*)$ where the left-hand side of (7) equals unity.

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In the rest of the paper we will assume that the survival and fecundity functions $\hat{s}(x)$, $\hat{p}(x)$ and $\hat{f}(x)$ are members of the Deriso Schnute family

$$\hat{h}(x) = (1 - \gamma\alpha x)^{1/\gamma} \tag{8}$$

where $\alpha > 0$ and $\gamma \leq 0$. Clearly $\hat{h}'(x) \leq 0$ and $\hat{h}(x) \in (0, 1]$. If $\gamma \to 0$, $\hat{h}(x) = \exp(-\alpha x)$ which is often referred to as the overcompensatory Ricker relation. If $\gamma = -1$, we have the compensatory Beverton and Holt relation $\hat{h}(x) = (1 + \alpha x)^{-1}$. For further discussion of the Deriso–Schnute family we refer to Bergh & Getz (1988), see also Wikan (1997, 1998).

3. Dynamical properties

3.1 THE AGE-STRUCTURED CASE

First we consider the ultimate precocious semelparous case $u_1 = u_2 = 1$ which means that (3) degenerates to an age-structured model. By use of the overcompensatory Ricker relation we then arrive at

$$x_{1,t+1} = F\,e^{-\alpha x_t}x_{2,t}$$
$$x_{2,t+1} = P\,e^{-\beta x_t}x_{1,t} \tag{9}$$

The inherent net reproductive number $R_0 = PF$ and in order to ensure that the origin is a repellor we assume $R_0 > 1$. The unique nontrivial fixed point of (9) is found to be

$$(x_1^*, x_2^*) = \left(\frac{1}{1 + aP}\,x^*,\ \frac{aP}{1 + aP}\,x^*\right) \tag{10}$$

where $a = R_0^{-(\beta/(\alpha+\beta))}$ and $x^* = x_1^* + x_2^* = (\alpha + \beta)^{-1}\ln R_0$.

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According to the Jury criteria (Murray, 1993), (10) is a stable fixed point whenever the inequalities

$$\beta x_1^* \left(1 + Pe^{-\beta x^*}\right) + \alpha x_2^* \left(1 + \alpha Fe^{-\alpha x^*}\right) > 0 \tag{11a}$$

$$(\beta - \alpha) \left(1 - Pe^{-\beta x^*}\right) x_1^* > 0 \tag{11b}$$

$$2 - (\beta x_1^* + \alpha x_2^*) > 0 \tag{11c}$$

hold.

Here, we may observe the following: The left-hand side of (11a) is always positive which means that (10) will never go unstable through a saddle node bifurcation. Assume $\beta > \alpha$. Then the left-hand side of (11b) is positive too so there will be no flip bifurcation. The left-hand side of (11c) is clearly positive in case of small equilibrium populations x_1^* and x_2^* but as they are increased (a consequence of an increase of R_0), (10) will eventually go unstable through a Hopf bifurcation at the threshold

$$x^* = \frac{2(1 + aP)}{\beta + \alpha aP} \tag{12}$$

or equivalently, at the threshold

$$R_0 = \exp\left[\frac{2(\alpha + \beta)(1 + aP)}{\beta + \alpha aP}\right] \tag{13}$$

Consequently, provided $\beta > \alpha$, the dynamics is a stable fixed point (x_1^*, x_2^*) in case of "small" values of x_1^* and x_2^* and nonstationary behaviour (governed by the Hopf bifurcation that occurs at instability threshold (12)) whenever the values of x_1^* and x_2^* are "large".

In somewhat more detail we have the following: If the difference $\beta - \alpha$ is small (for example $\beta = 1.1$ and $\alpha = 1.0$) we find that close to (but above) the bifurcation threshold,

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the dynamics is restricted on an invariant curve which surrounds the unstable fixed point. Through further enlargement of R_0 we still find the invariant curve but eventually the curve becomes kinked which signals that we are on the onset to chaos. This is shown in Fig. 1. In case of higher R_0 values the curve disappears and the points in state space appear to be randomly distributed which suggests that a subcritical bifurcation has occurred. Note that there is no sign of periodic behaviour whenever $\beta - \alpha$ is small.

If the difference $\beta - \alpha$ is large (for example $\beta = 2$, $\alpha = 1$) there exists an exact 3-period orbit in large parts of parameter space. An example of such an orbit is given in Fig. 2. The 3-cycle is not established through frequency locking from the invariant curve, see Wikan & Mjølhus (1996). It is created as the third iterate of (9) undergoes a saddle node bifurcation at a threshold which is lower than the threshold (12). Therefore there are regions in parameter space where the 3-cycle coexists with both the stable fixed point (10) and (in case of larger R_0 values) the invariant curve. Also here we experience chaotic dynamics if the R_0 values become sufficiently high, cf. Fig. 3 where a chaotic attractor is shown. There is no sign of periodicity in the chaotic regime except for small parameter windows where periodic orbits have been detected.

Finally it should also be mentioned that if $\alpha = 0$ which implies that there is only density dependence in the survival term in (9), four-periodic behaviour, either exact or approximate, is the outcome in large regions of parameter space the chaotic regime included, see Wikan (1998).

Next, consider the case $\beta \leq \alpha$. The crucial point here is that the left-hand side of (11b) now becomes negative (or equal to zero if $\alpha = \beta$) which in turn implies that the

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fixed point (10) will always be unstable. Since (11b) is associated with the possibility that (10) shall undergo a flip bifurcation it is natural to seek for a stable 2- cycle in case of R_0 is small. Evidently, such a 2-cycle may be obtained from the relations

$$x_{1,t+2} = R_0 \exp(-\beta x_t) \exp(-\alpha x_{t+1}) x_{1,t}$$

$$x_{2,t+2} = R_0 \exp(-\alpha x_t) \exp(-\beta x_{t+1}) x_{2,t}$$

(14)

and here there are two possibilities. 1) $x_t = x_{t+2}$ which leads to the trivial 2-cycle where the unstable fixed point (10) is the repeating point in the cycle. 2) The points are on the form $(\hat{x}_1, \hat{x}_2) = (A, 0)$ or $(0, B)$ which means that only one age class is populated at each time. A may be found by means of numerical methods from the relation

$$\beta A + \alpha P e^{-\beta A} A = \ln R_0$$

(15)

which in turn implies

$$B = P e^{-\beta A} A$$

(16)

(Note that if no density dependence in the survival is assumed (i.e. $\beta = 0$) we obtain $A = (\alpha P)^{-1} \ln R_0$ and $B = \alpha^{-1} \ln R_0$.)

Through numerical simulations we have verified that an increase of R_0 leads to a series of flip bifurcations creating orbits of period 2^k, $k > 1$. Eventually, beyond the accumulation point of the flip bifurcations, the dynamics becomes chaotic. We emphasize that both in the finite period case as well as in the chaotic regime only one age class is populated at each time. These findings are summarized in the bifurcation diagram, Fig. 4.

Following Davydova *et al.* (2003) and Solberg (1998) we shall from now on denote dynamics where only one age class is populated at each time for SYC (Single Year Class)

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dynamics. Bulmer (1977) appears to be the first to have noticed SYC phenomena in theoretical models. Results concerning SYC dynamics may also be obtained in Wikan (1997), Behncke (2000) and Mjølhus *et al.* (2005). Davydova *et al.* (2003) perform a thorough discussion and give precise results of conditions which lead to SYC dynamics and conditions where both age classes may coexist. An important finding in Mjølhus *et al.* (2005), where several age classes with fecundity $f(x)$ (x = total population) restricted to the last age class only are considered, is that small perturbing populations inserted into empty age classes will experience a higher population pressure x in their reproductive phase than the main population and will therefore have a subcritical recruitment and consequently they will vanish in the long run.

Regarding our model (9) where both the fecundity and survival probability are functions of the total population it is natural to conclude that it is the "strength" of density dependence which will decide whether the two age classes may coexist or not. If $\alpha > \beta$ SYC dynamics is the outcome. On the other hand, if $\alpha < \beta$ the result is coexistence.

A final point is that the results presented above seem to be independent of the choice of fecundity or survival function. Indeed, if we replace the Ricker relation in (9) with the compensatory Beverton and Holt relation we arrive at

$$
\begin{aligned}
x_{1,t+1} &= \frac{F}{1 + \alpha x_t} \, x_{2,t} \\
x_{2,t+1} &= \frac{P}{1 + \beta x_t} \, x_{1,t}
\end{aligned}
\tag{17}
$$

At equilibrium

$$
(x_1^*, x_2^*) = \left(\frac{1 + \beta x^*}{1 + \beta x^* + P} \, x^*, \ \frac{P}{1 + \beta x^* + P} \, x^* \right)
\tag{18}
$$

where

$$x^* = \frac{1}{2\alpha\beta}\left[\sqrt{(\alpha - \beta)^2 + 4\alpha\beta R_0} - (\alpha + \beta)\right]$$

The criteria for (18) to be stable are

$$\frac{\alpha x_2^*}{1 + \alpha x^*}\left(1 + \frac{F}{1 + \alpha x^*}\right) + \frac{\beta x_1^*}{1 + \beta x^*}\left(1 + \frac{P}{1 + \beta x^*}\right) > 0 \tag{19a}$$

$$\frac{\beta - \alpha}{R_0}\left(1 - \frac{P}{1 + \beta x^*}\right)x_1^* > 0 \tag{19b}$$

$$2 - \left[\frac{\beta x_1^*}{1 + \beta x^*} + \frac{\alpha x_2^*}{1 + \alpha x^*}\right] > 0 \tag{19c}$$

and here we observe that whenever $\beta > \alpha$ all three left-hand sides of (19) are positive. Thus (18) is a stable fixed point where both age classes are populated. On the other hand, if $\beta \leq \alpha$, (19b) is always violated so (18) is never stable and by the same argument as in the Ricker case we find that SYC dynamics is the only outcome.

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Let us now extend the age-structured model (9) to the corresponding stage-structured case, and in order to compare our results directly with the results of Neubert & Caswell (2000) we simplify (3) by letting $S = 1$ and $P = u_1 S$ and consider the system

$$x_{1,t+1} = (1 - u_1)x_{1,t} + F e^{-\alpha x_t}x_{2,t}$$

$$x_{2,t+1} = u_1 e^{-\beta x_t}x_{1,t} + (1 - u_2)x_{2,t} \tag{20}$$

Thus, the main difference between our model and the Neubert–Caswell model is that we consider the combined effect of density-dependent survival and density-dependent fecundity which they do not. The unique nontrivial equilibrium may be expressed as

$$(x_1^*, x_2^*) = \left(\frac{u_2}{u_2 + u_1 e^{-\beta x^*}}\, x^*,\ \frac{u_1 e^{-\beta x^*}}{u_2 + u_1 e^{-\beta x^*}}\, x^*\right) \tag{21}$$

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where $x^* = (\alpha + \beta)^{-1} \ln R_0$ and R_0 is defined through (6). (21) is a stable equilibrium as long as the Jury conditions

$$u_1 u_2 (\beta x_1^* + \alpha x_2^*) + \beta u_1^2 e^{-\beta x^*} x_1^* + \alpha u_2 F e^{-\alpha x^*} x_2^* > 0 \tag{22a}$$

$$2[2 - u_1 - u_2] + u_1 u_2 (\beta x_1^* + \alpha x_2^*) - \beta(2 - u_1) u_1 e^{-\beta x^*} x_1^* - \alpha(2 - u_2) F e^{-\alpha x^*} x_2^* > 0 \tag{22b}$$

$$u_1 + u_2 - u_1 u_2 (\beta x_1^* + \alpha x_2^*) + \beta u_1 (1 - u_1) e^{-\beta x^*} x_1^* + \alpha F (1 - u_2) e^{-\alpha x^*} x_2^* > 0 \tag{22c}$$

hold. The left-hand side of (22a) is always positive, thus we can as in the age-structured case exclude the possibility that the fixed point will become unstable through a saddle node bifurcation. If (22b) or (22c) are violated, (21) will undergo a flip or a Hopf bifurcation at instability threshold. It is further obvious that in case of sufficiently small equilibrium populations x_1^*, x_2^* the dominating term in (22b) is $2[2 - u_1 - u_2]$ and the corresponding term in (22c) is $u_1 + u_2$. Since both these terms are positive we conclude that (21) is a stable fixed point in case of x_1^*, x_2^* small and moreover, in contrast to the age-structured case we may rule out the possibility of SYC dynamics.

3.2 THE PRECOCIOUS SEMELPAROUS CASE

Regarding the nonstationary dynamics, let us first concentrate on the precocious semelparous case ($u_1 \to 1$, $u_2 \to 1$). Since both u_1 and u_2 are close to unity we may assume that $u_1 = u_2 = u$ and from the results of the analysis of the age-structured model we find it natural to deal with the cases $\alpha < \beta$, $\alpha = \beta$ and $\alpha > \beta$ separately.

Assume $\alpha = \beta = 1$ (=1 because when $\alpha = \beta$ both of them can be scaled into the

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population). The conditions (22b,c) now become

$$2(1 - u)(2 - ux^*) > 0 \tag{23b}$$

$$u[2 - (2u - 1)x^*] > 0 \tag{23c}$$

and evidently, whenever $u > 1/2$ it is clear that through an increase of x^* the left-hand side of (23b) will become negative prior to the left-hand side of (23c). Thus the only way from stability to instability goes through a flip bifurcation.

In order to exemplify the dynamics beyond the bifurcation threshold, consider the parameter set $u_1 = u_2 = 0.9$. Then from (23b) the flip occurs when $x^* = 2/u$ which in turn implies that $F = 76.637$ and in case of larger F values we find an exact 2-period orbit. (For example $F = 100$ leads to the 2-cycle (1.29, 0.12), (3.11, 0.29).) Further numerical experiments show that the qualitative behaviour of 2-cycles persists even if we multiply F by a factor 10. Hence it is natural to conclude that an increase of x^* (of F) acts in a "weak" destabilizing fashion.

Next, consider the case $\alpha > \beta$ (and still $u_1 = u_2 = u$ close to unity). The conditions (22b,c) may now be cast in the form

$$4(1 - u) + \frac{x^*}{1 + e^{-\beta x^*}} \left\{ [(\alpha + \beta)u^2 - 2\alpha u] + e^{-\beta x^*}[(\alpha + \beta)u^2 - 2\beta u] \right\} > 0 \tag{24b}$$

$$2u + \frac{x^*}{1 + e^{-\beta x^*}} \left\{ [\alpha u - (\alpha + \beta)u^2] + e^{-\beta x^*}[\beta u - (\alpha + \beta)u^2] \right\} > 0 \tag{24c}$$

When x^* grows (for example through an increase of F) the dominating terms on the

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left-hand sides of (24b,c) are

$$4(1 - u) - [2\alpha - (\alpha + \beta)u]ux^* \tag{25b}$$

$$2u - [(\alpha + \beta)u - \alpha]ux^* \tag{25c}$$

and it is obvious that (25b) is (much) smaller than (25c). Consequently, the dynamics beyond the instability threshold is governed by the flip bifurcation here too.

However, the nonstationary dynamics whenever $\alpha > \beta$ is much richer than in the "symmetric" case $\alpha = \beta$. Through an enlargement of x^* (or F) we find periodic orbits of period 2^k, $k = 1$, and eventually, beyond the accumulation point of the flip bifurcation sequence, the dynamics becomes chaotic. This is exemplified in Fig. 5. (Note that each of the branches of the attractor is visited only once every second iteration so even if the dynamics is chaotic a kind of 2-periodicity is still preserved.)

Finally, consider the remaining situation $\alpha < \beta$. As the equilibrium population x^* is increased the dominating terms on the left-hand sides of inequalities (24b,c) are

$$4(1 - u) + [(\alpha + \beta)u - 2\alpha]ux^* \tag{26b}$$

$$2u - [(\alpha + \beta)u - \alpha]ux^* \tag{26c}$$

and evidently, in most of parameter space the first term to become negative is (26c). Thus the general case is that (21) goes unstable through a Hopf bifurcation which means that just above the bifurcation threshold the dynamics is restricted on an invariant curve as displayed in Fig. 6. Through further enlargement of x^* the only stable attractor is an exact 3-period orbit which is created in the same way as in the age-structured case (cf. our

previous discussion). We also find regions in parameter space where the 3-cycle coexists with the stable equilibrium and the invariant curve.

3.3 THE DELAYED SEMELPAROUS CASE

Let us now focus on the delayed semelparous case which is characterized by $u_2 \to 1$, $0 < u_1 < 1$. If $u_2 = 1$ is assumed (we have performed lots of simulations where $u_2 = 0.8$ or 0.9 and the dynamics found in these simulations is qualitatively similar to the $u_2 = 1$ case) the stability criteria (22b,c) may be expressed as

$$2(1 - u_1) + \frac{u_1 x^*}{1 + u_1 e^{-\beta x^*}} \left\{ (\beta - \alpha) + e^{-\beta x^*}(\alpha - 2\beta + u_1 \beta) \right\} > 0 \qquad (27b)$$

$$1 + u_1 + \frac{u_1 x^*}{1 + u_1 e^{-\beta x^*}} \left\{ e^{-\beta x^*} [\beta(1 - u_1) - \alpha] - \beta \right\} > 0 \qquad (27c)$$

If $u_1 \to 0$, clearly both left-hand sides of (27b,c) are positive in case of x^* sufficiently small. Hence (x_1^*, x_2^*) is stable. For larger values of u_1 (for example $u_1 = 0.4$) nonstationary dynamics may occur. Indeed, if $\beta \geq \alpha$ and x^* is large, (27c) contains a dominant negative term $(-u_1 \beta x^*)$ so when x^* becomes sufficiently large the equilibrium goes unstable through a Hopf bifurcation. We have verified numerically the existence of an invariant curve but no chaotic dynamics has been detected. On the other hand, if $\alpha \gg \beta$ and x^* is large, (27b) contains a dominant negative term $u_1(\beta - \alpha)x^*$ so eventually, an enlargement of x^* will now lead to a flip bifurcation. Numerically, 2-periodic orbits have been identified in case of x^* large but neither orbits of period 2^k, $k > 1$, nor chaotic dynamics have been detected.

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3.4 THE PRECOCIOUS ITEROPAROUS CASE

The first iteroparous case to consider is the precocious one $u_1 \to 1$, $0 < u_2 < 1$ and as we have proved earlier (x_1^*, x_2^*) is stable whenever x^* is sufficiently small.

As x^* becomes larger (through an increase of F) we find in the special case $u_1 = 1$ that the stability criteria (22b,c) asymptotically may be expressed as

$$2(1 - u_2) + x^*[u_2(\alpha + \beta) - 2\alpha] > 0 \tag{28b}$$

$$1 + u_2 + x^*[\alpha - u_2(\alpha + \beta)] > 0 \tag{28c}$$

Suppose $u_2 \to 0$. Then (by L'Hopital's rule) $x^* u_2 \to 0$ which in turn implies that inequality (28c) will never be violated. Consequently, the only transfer from stability to instability goes through a (supercritical) flip bifurcation as (28b) is violated. In case of larger values of u_2 ($u_2 \to 1/2$) the same conclusion holds if $\alpha \geq \beta$ but if $\beta \gg \alpha$ (28c) is violated prior to (28b) and an attracting invariant curve is established when (x_1^*, x_2^*) fails to be stable. Numerically, the findings reported above have been verified through lots of simulations where parameter values $0.8 \leq u_1 \leq 1.0$, $0 \leq u_2 \leq 0.5$ have been used. If $\alpha \geq \beta$ we have found orbits of period 2^k, $k > 1$, as well as chaotic dynamics. When β becomes larger than α the dynamics becomes "more stable" in the sense that only orbits of period 2^k, $k > 1$, have been detected beyond the bifurcation threshold. (If $\alpha = 1$, $\beta = 4$, $u_1 = 0.9$, $u_2 = 0.4$) only cycles of period 2 have been identified.) In case of even higher values of β invariant curves are the only outcome.

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3.5 THE DELAYED ITEROPAROUS CASE

The final case to analyse is the delayed iteroparous one which occurs when both u_1 and u_2 are small numbers.

In the symmetric case $\alpha = \beta = 1$ and $u_1 = u_2 = u$ where u is small $(u < 1/2)$ the stability criteria are given by (23b,c) and since the left-hand side of (23c) is always positive we may exclude the possibility of a Hopf bifurcation at instability threshold. Thus the only way that (x_1^*, x_2^*) may become unstable is through a flip bifurcation at the threshold $x^* = 2/u$. Beyond the threshold there are period-2 cycles. We have not found orbits of period 2^k, $k > 1$, and it should also be mentioned that the region where (x_1^*, x_2^*) is stable is large.

If $\alpha > \beta$ we experience much of the same qualitative picture as earlier. The dynamics becomes more unstable so periodic orbits of 2^k, $k > 1$, as well as chaotic dynamics may be observed.

If $\alpha < \beta$ it is obvious that (25c) < (25b). Hence there are nonperiodic orbits restricted to an invariant curve in the unstable parameter region.

4. Discussion

In the first part of this paper we proved under quite general conditions that the basic model (3) is permanent. Hence the population will neither go extinct nor experience explosive oscillations. Subsequently we revealed and studied various dynamical properties of semelparous and iteroparous species. Regarding the latter we shall now interpret and unify our results.

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In Table 1 we show the equilibrium population x^* at instability threshold for some specified values of u_i, α and β. x^* has been calculated by use of the stability criteria from Section 3.

There is a lot of evidence, see Guckenheimer *et al.* (1977), Levin & Goodyear (1980), Bergh & Getz (1988), Silva & Hallam (1993), Wikan & Mjølhus (1996), Neubert & Caswell (2000) and Davydova *et al.* (2003), that an increase of the total equilibrium population in general leads to nonstationary dynamics provided the survival or (and) the recruitment functions are of the Ricker type (but see Mjølhus *et al.* (2005) for a counter example).

Thus, by use of the size of x^* as a stability criterion, Table 1 suggests that species with iteroparous life histories are more stable than species which have semelparous life histories. This is also supported by the results obtained from the age-structured model (9) which may be regarded as the most "extreme" precocious semelparous case. Recall that the equilibrium (10) was found to be unstable for all $R_0 > 1$ provided $\alpha \geq \beta$. Moreover, both in Higgins *et al.* (1997) where a delay difference equation model was considered as well as in Neubert & Caswell (2000) similar conclusions were obtained. Therefore, as proposed by Neubert & Caswell (2000), it is tempting to suggest that our findings

TABLE 1
x^* at instability threshold

	Semelparous		Iteroparous	
	Delayed	Precocious	Delayed	Precocious
	$u_1 = 0.4 \quad u_2 = 0.9$	$u_1 = u_2 = 0.9$	$u_1 = u_2 = 0.4$	$u_1 = 0.9 \quad u_2 = 0.4$
$\alpha = 2 \quad \beta = 1$	$x^* = 2.61$	$x^* = 0.68$	$x^* = 2.27$	$x^* = 1.04$
$\alpha = \beta = 1$	$x^* = 3.79$	$x^* = 2.22$	$x^* = 5.00$	$x^* = 1.74$
$\alpha = 1 \quad \beta = 2$	$x^* = 1.91$	$x^* = 1.16$	$x^* > 10.0$	$x^* = 1.86$

illustrate a fairly general ecological principle, namely that iteroparous species are more stable than semelparous species.

From the findings presented in Table 1 there is also a clear tendency that delayed semelparous species tend to be more stable than precocious semelparous species and that the same conclusion also applies in the iteroparous case. In order to explore this further, let us now turn to the nonstationary dynamics. In Table 2 we summarize the dynamics found in the previous section.

TABLE 2
Possible dynamical outcomes

| | Semelparous ($u_1 \to 1$) | | Iteroparous ($0 < u_2 < 1$) | |
	Delayed ($0 < u_1 < 1$)	Precocious ($u_1 \to 1$)	Delayed ($0 < u_1 < 1$)	Precocious ($u_1 \to 1$)
$\alpha > \beta$	$S \to 2$	$S \to 2^k,\ k \geq 1 \to C$	$S \to 2^k,\ k \geq 1 \to C$	$S \to 2^k,\ k \geq 1 \to C$
$\alpha = \beta$	$S \to I \to 3$	$S \to 2$	$S \to 2$	$S \to 2^k,\ k \geq 1 \to C$
$\alpha < \beta$	$S \to I \to 4$	$S \to I \to 3 \to C$	$S \to I$	$S \to 2^k,\ k \geq 1$

The table should be read in the following way: Consider the sequence $S \to 2^k$, $k \geq 1 \to C$. This means that when the equilibrium population is small it is stable (indicated by S). When the equilibrium population is increased (indicated by $\to$) we find periodic orbits of 2, 4, 8 and so on (indicated by 2^k, $k \geq 1$). The symbol C means chaos. I refers to nonperiodic orbits restricted to an invariant curve while 2, 3 and 4 refer to orbits of period two, three and four respectively. It should also be mentioned that in the chaotic regime C we find several examples of parameter windows where the dynamics is periodic but typically the period is large.

From Table 2 it is natural to conclude that species with precocious life histories are

more likely to exhibit chaotic oscillations than species with delayed life histories. Thus by use of possible chaotic dynamics as a stability criterion we arrive at the same conclusion as we found when the size of x^* was used as a stability criterion. Species with precocious life histories are the most unstable ones. Again we find that our conclusions are in good agreement with Neubert & Caswell (2000). (Neubert and Caswell consider several models, some with density-dependent recruitment, others with density-dependent survival or growth, but unlike us they do not consider density-dependent recruitment and density-dependent survival at the same time.) On the other hand, our conclusions are in contrast to the findings in Higgins *et al.* (1997). In the latter paper (where they consider a delay difference equation) they concluded that species with precocious life histories were more stable, especially in iteroparous species.

It is not obvious what causes this discrepancy. If we for a moment turn to age-structured models with density-dependent recruitment, see for example Levin & Goodyear (1980) or Wikan & Mjølhus (1996) one common conclusion is that an increase of the number of age classes acts as a stabilizing effect. Regarding our main model (3), the age-structured model roughly corresponds to the case u_2 small and u_1 large, thus to the precocious iteroparous case. Hence the agreement between the age-structured case and Higgins *et al.* (1997) appears to be better than the agreement which Neubert and Caswell and we have with the age-structured case. However, in the age-structured models by Wikan & Mjølhus (1995) and Wikan (1998) where the recruitment were density independent and the year-to-year survival probabilities were density dependent an increase of the number of age classes was not found to act in a stabilizing fashion so the agreement with

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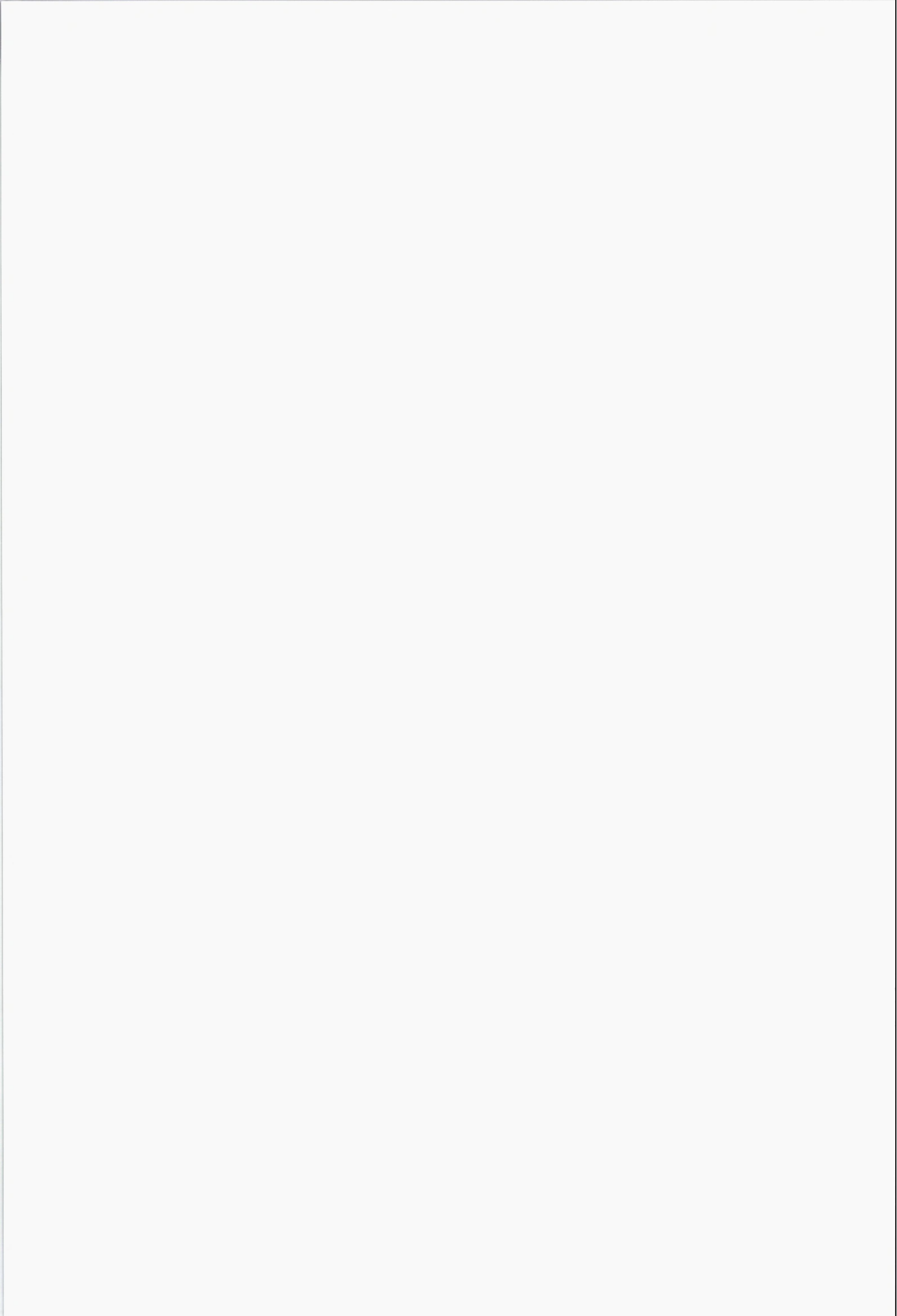
Higgins *et al.* (1997) is not good in this case. Thus, at present, we find it difficult to formulate some kind of general ecological principle regarding the dynamics of species with delayed life histories compared to species with precocious life histories. Since different models give different conclusions details appear to matter and there is a need for further studies on this topic, especially studies which include more density-dependent effects.

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APPENDIX

Proof of Theorem 1 in the main text

Clearly, $(x_1^*, x_2^*) = (0,0)$ is a fixed point of model (3). The Jacobian (evaluated at $(0,0)$) equals the matrix

$$A_0 = \begin{pmatrix} (1-u_1)S & F \\ P & 1-u_2 \end{pmatrix}$$

and the corresponding eigenvalue equation becomes

$$\lambda^2 - [(1-u_1)S + (1-u_2)]\lambda + (1-u_1)(1-u_2)S - PF = 0$$

From the Jury criteria (Murray, 1993), it is now straightforward to show that whenever

$$\frac{PF}{u_2(1-(1-u_1)S)} = R_0 > 1$$

the magnitude of the dominant eigenvalue of A_0 is larger than unity. Thus the origin is a repellor.

Further, the restrictions on the parameters and functions given in (2) ensure that A_0 is irreducible and that A_x is non-negative for all $(x_1, x_2) \in \mathbb{R}_+^2$. Consequently, (3) is $\mathbb{R}_+^2 \setminus \{0\}$ forward invariant.

It remains to prove that the population density does not explode, i.e. that (3) is a dissipative model. From Kon *et al.* (2004) we apply the following definition of dissipativeness:

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Definition

Model (3) is said to be dissipative if there exists a compact set $X \subset \mathbb{R}_+^2$ such that for all $\bar{x}_0 \in \mathbb{R}_+^2$ there exists a $t^M = t^M(\bar{x}_0)$ satisfying $x_t \in X$ for all $t \geq t^M$.

—

We shall now show that if one of $\hat{p}(x)x_1$ or $\hat{f}(x)x_2$ is bounded from above, then (3) is dissipative. First, assume that $\hat{p}(x)x_1 \leq K_0$. Then, from (3)

$$x_{2,t+1} \leq PK_0 + (1 - u_2)x_{2,t}$$

and (by induction)

$$x_{2,t} \leq (1 - u_2)^t x_{2,0} + \frac{PK_0}{u_2}$$

Then, there exists $t^a = t^a(x_{2,0})$ such that for $t > t^a$

$$x_{2,t} \leq \frac{2PK_0}{u_2} = K_1$$

Further, in case of $t > t^a$, we have from (3)

$$x_{1,t+1} \leq (1 - u_1)Sx_{1,t} + FK_1$$

and again by induction we have

$$x_{1,t} \leq (1 - u_1)^t S^t x_{1,0} + \frac{FK_1}{1 - (1 - u_1)S}$$

Then, there exists $t^B = t^B(x_{1,0})$ such that for $t > t^B(x_{1,0})$

$$x_{1,t} \leq \frac{2FK_1}{1 - (1 - u_1)S} = K_2$$

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Take $t^M = \max\{t^A, t^B\}$ and $K = \max\{K_1, K_2\}$. Then for $t \geq t^M$, $x_{1,t} \leq K$ and $x_{2,t} \leq K$.

Hence, (3) is dissipative if $\hat{p}(x)x_1$ is bounded from above.

Next, assume $\hat{f}(x)x_2 \leq K_0$. From (3)

$$x_{1,t+1} \leq (1 - u_1)Sx_{1,t} + FK_0$$

and by induction

$$x_{1,t} \leq (1 - u_1)^t S^t x_{1,0} + \frac{FK_0}{1 - (1 - u_1)S}$$

Then, there exists $t^A = t^A(x_{1,0})$ such that for $t > t^A$

$$x_{1,t} \leq \frac{2FK_0}{1 - (1 - u_1)S} = K_1$$

Further, in case of $t > t^A$, (3) also gives

$$x_{2,t+1} \leq PK_1 + (1 - u_2)x_{2,t}$$

and once again (by induction) we find that for $t > t^B(x_{2,0})$

$$x_{2,t} \leq \frac{2PK_1}{u_2} = K_2$$

Finally, take $t^M = \max\{t^A, t^B\}$ and $K = \max\{K_1, K_2\}$. Then for $t \geq t^M$, $x_{1,t} \leq K$, $x_{2,t} \leq K$. This concludes the proof of Theorem 1.

Figure Captions

FIG. 1: An attractor generated by (9). Parameter values $F = 60$, $P = 0.8$, $\alpha = 1$, $\beta = 1.1$.
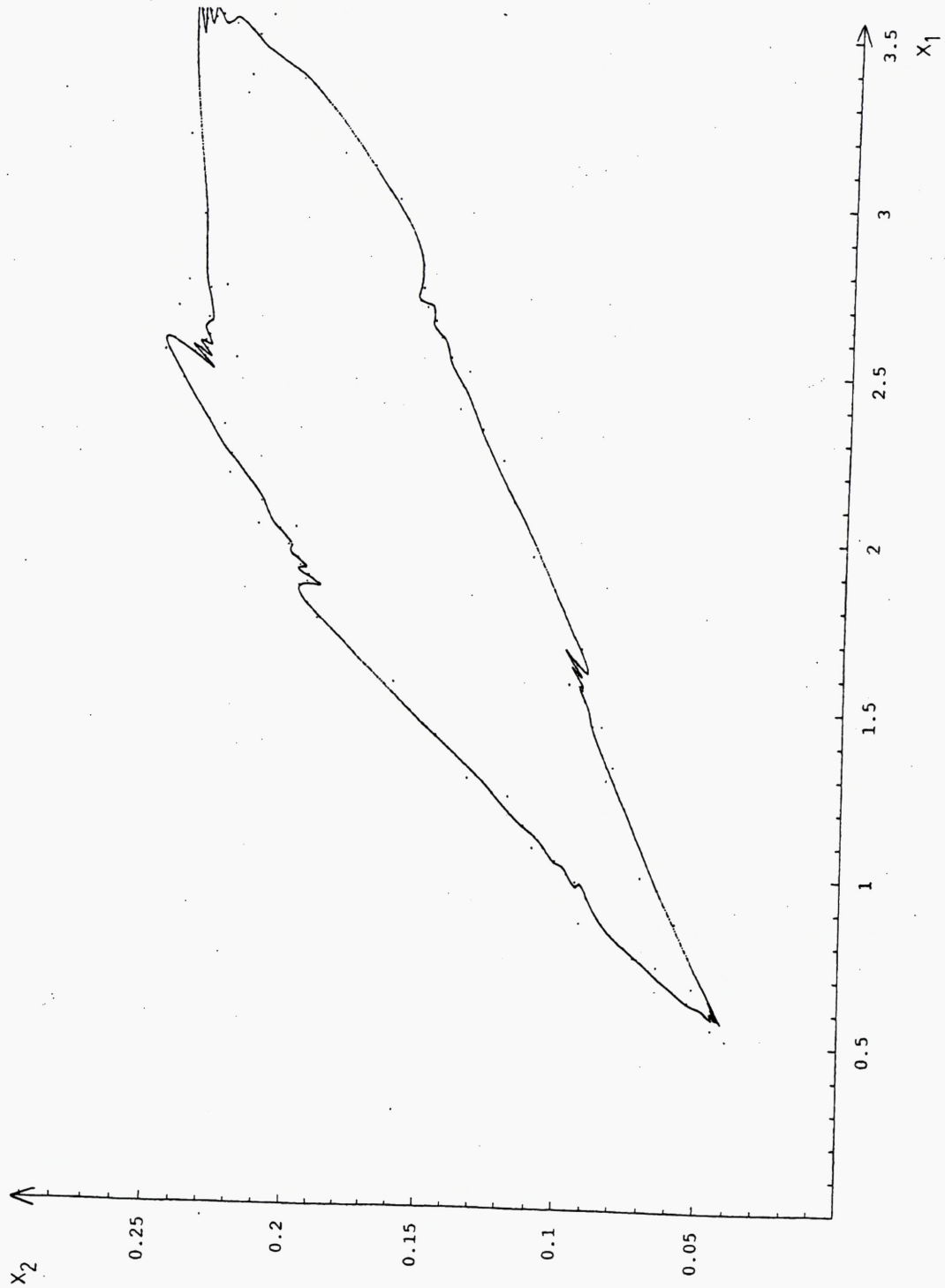
FIG. 2: An exact 3-period orbit. Parameter values $F = 25$, $P = 0.8$, $\alpha = 1$, $\beta = 2$.
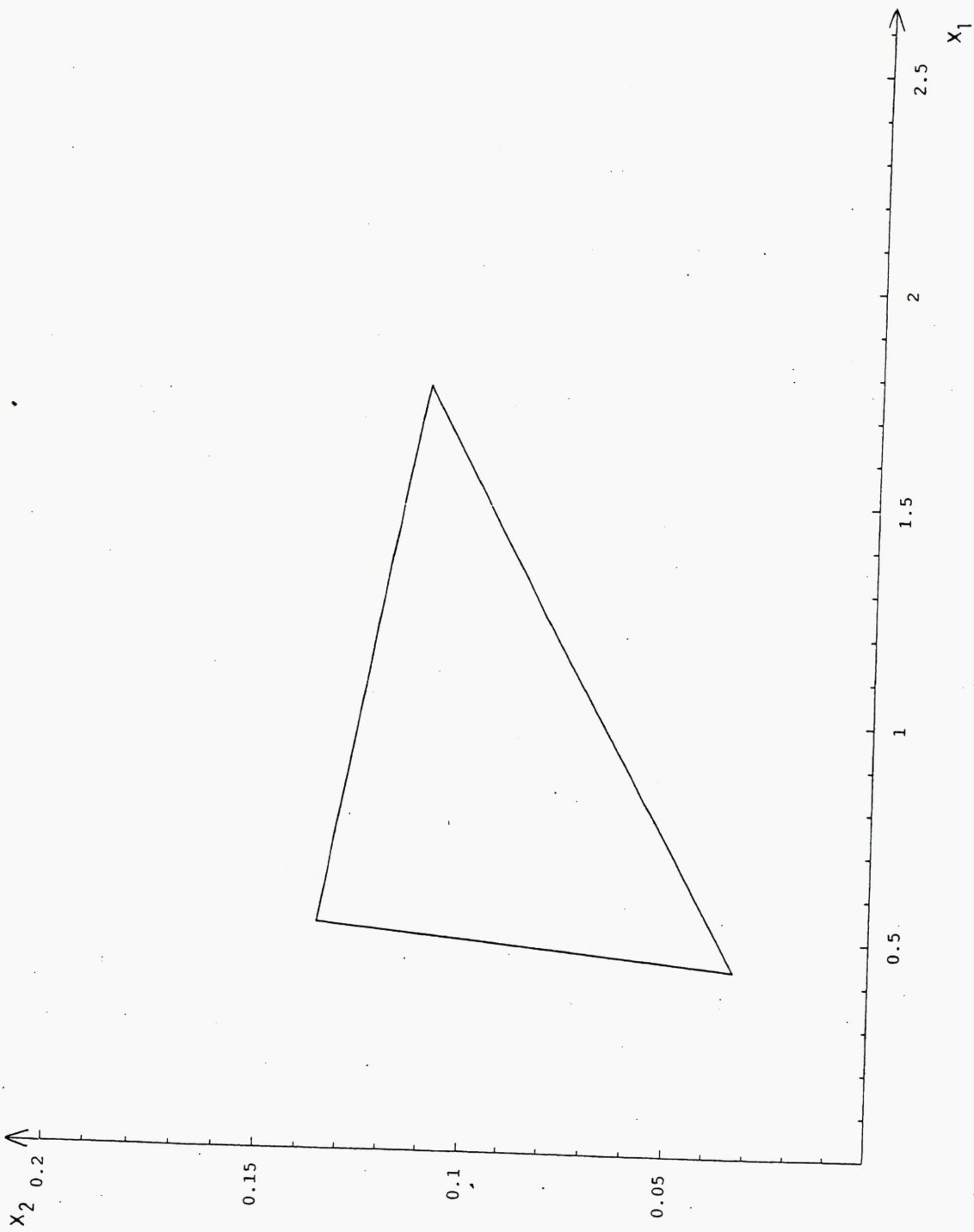
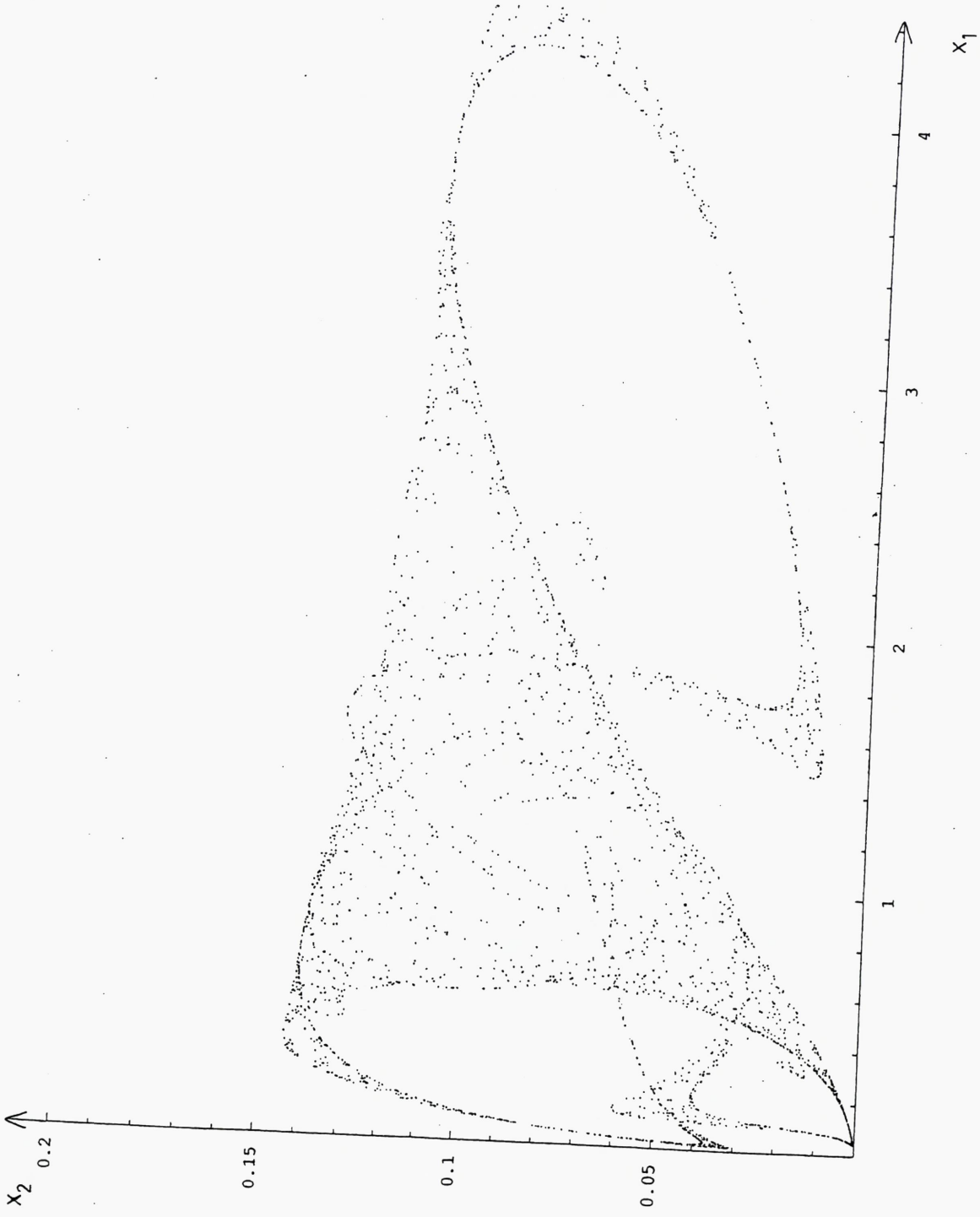FIG. 3: Chaotic dynamics. Parameter values as in Fig. 2 except $F = 60$.

FIG. 4: The bifurcation diagram generated by map (9). $\alpha = 2$, $\beta = 1$.
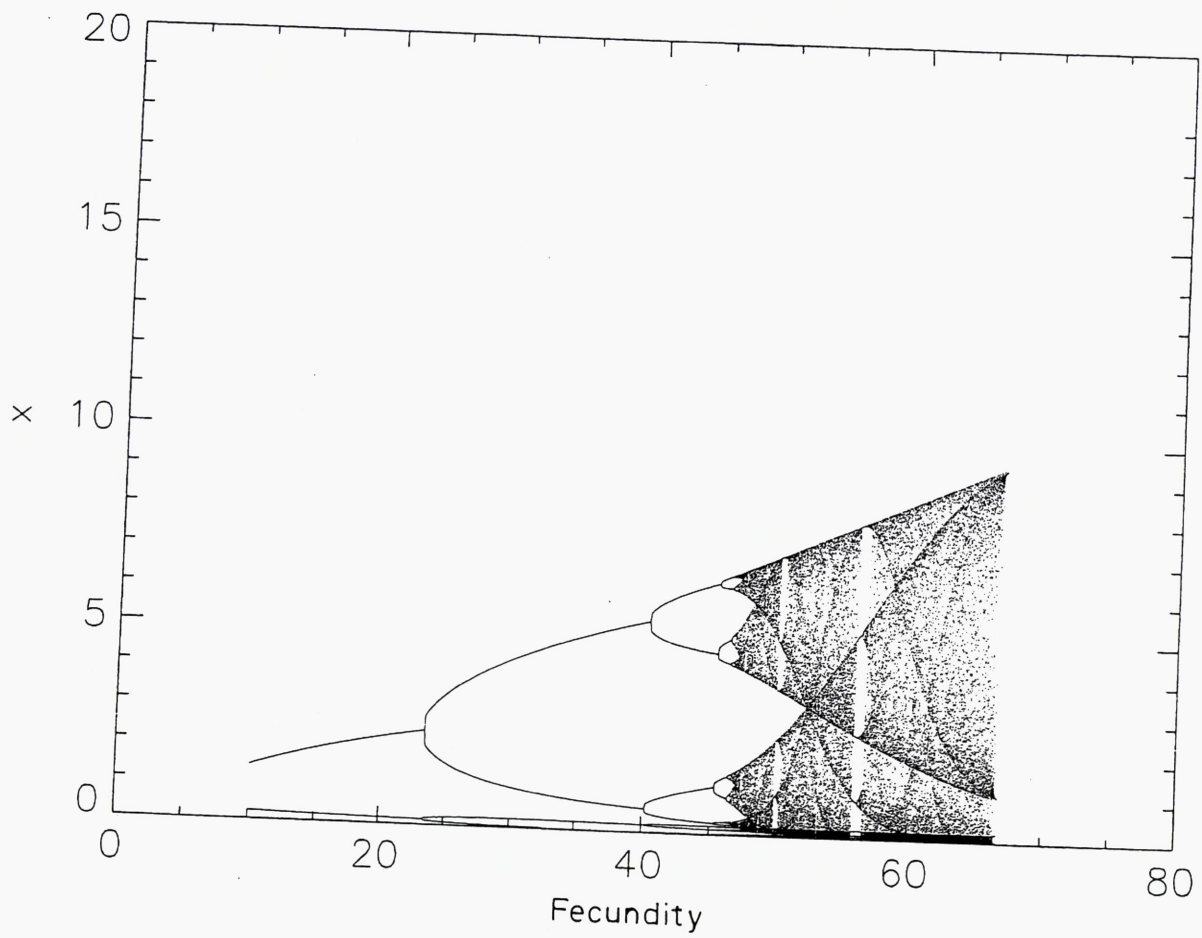
FIG. 5: An attractor generated by (20) in the case $\alpha = 2$, $\beta = 1$, $F = 60$, $u_1 = u_2 = 0.9$.
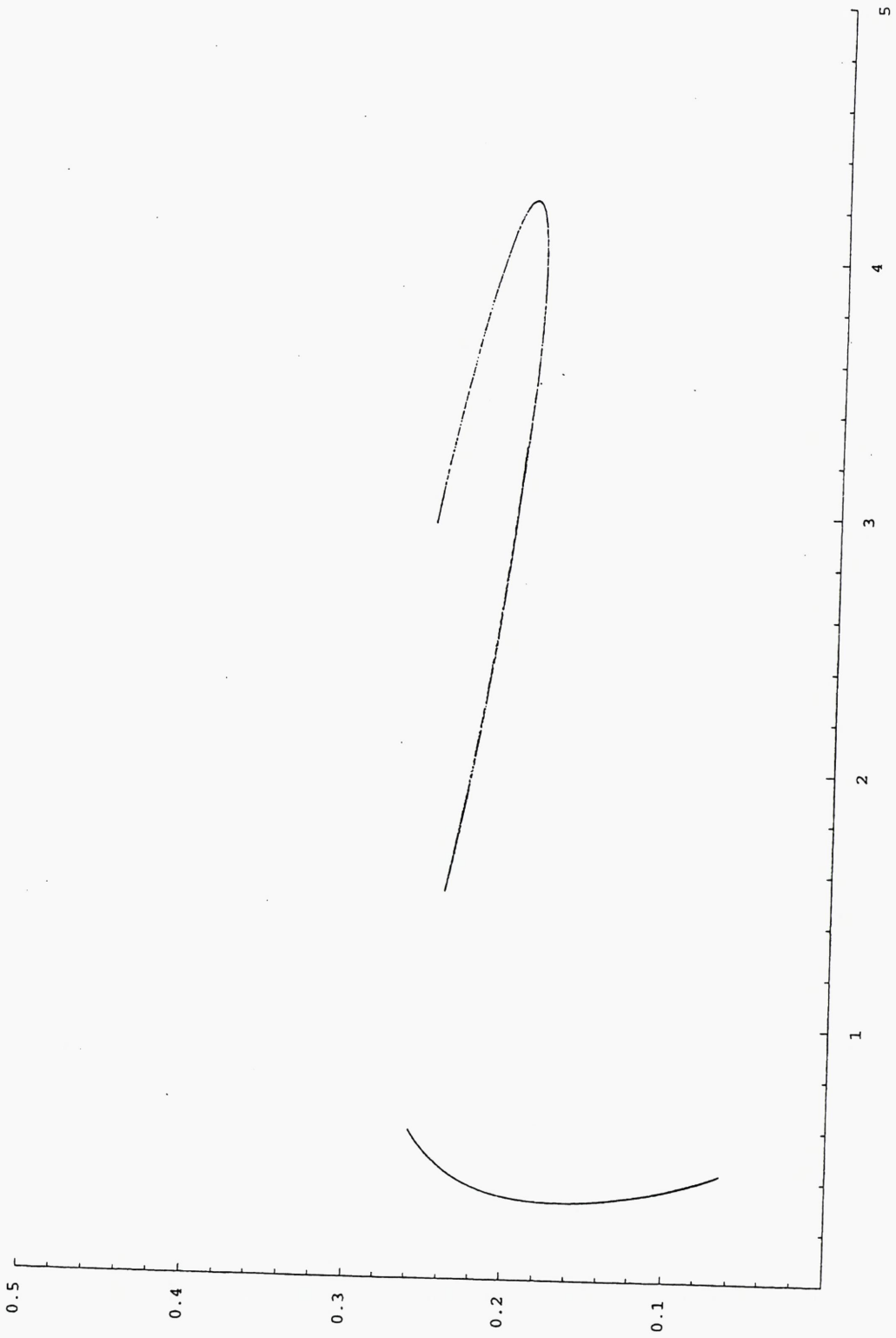
FIG. 6: An invariant curve generated by (20) in the case $\alpha = 1$, $\beta = 1.5$, $F = 60$, $u_1 = u_2 = 0.9$.
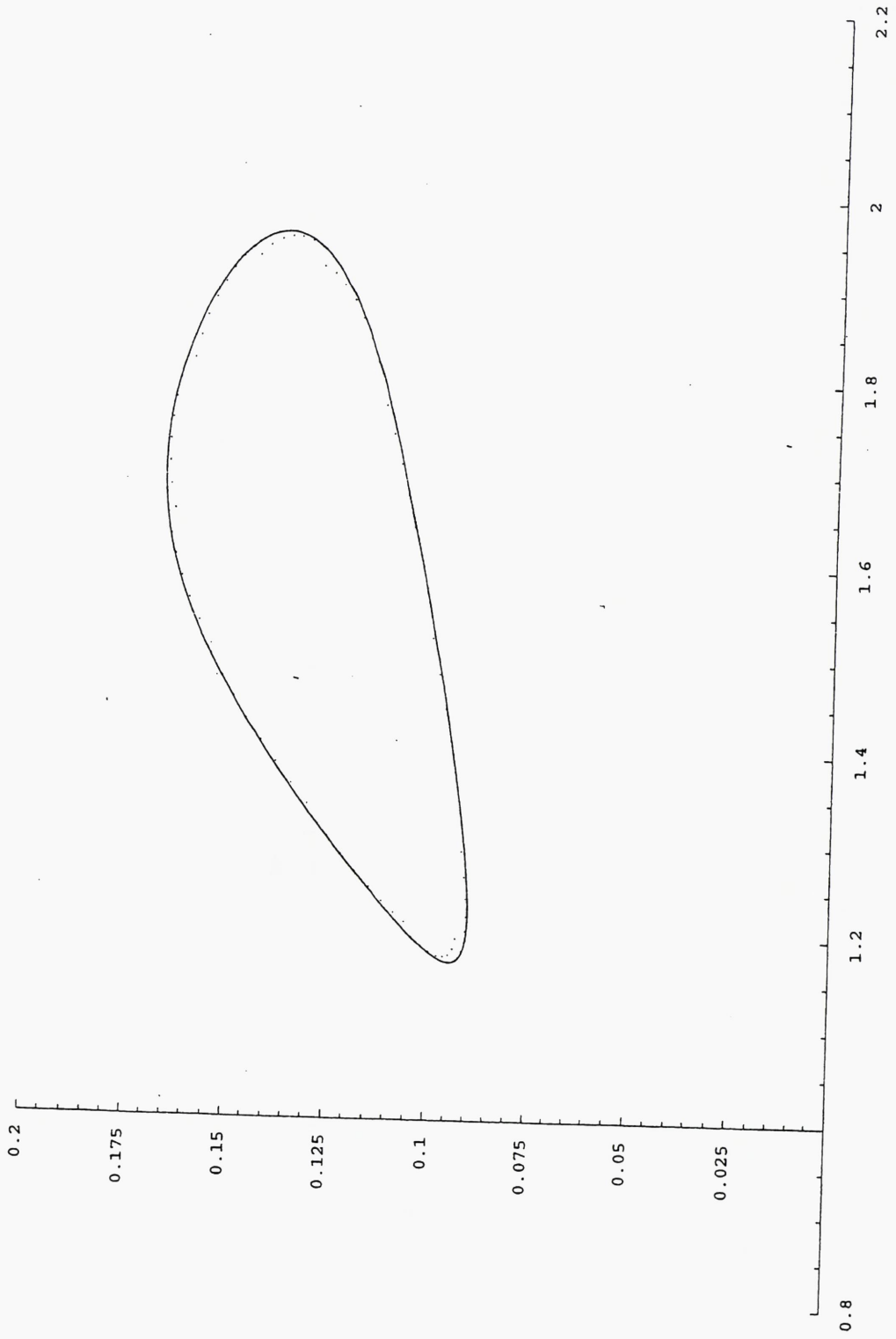
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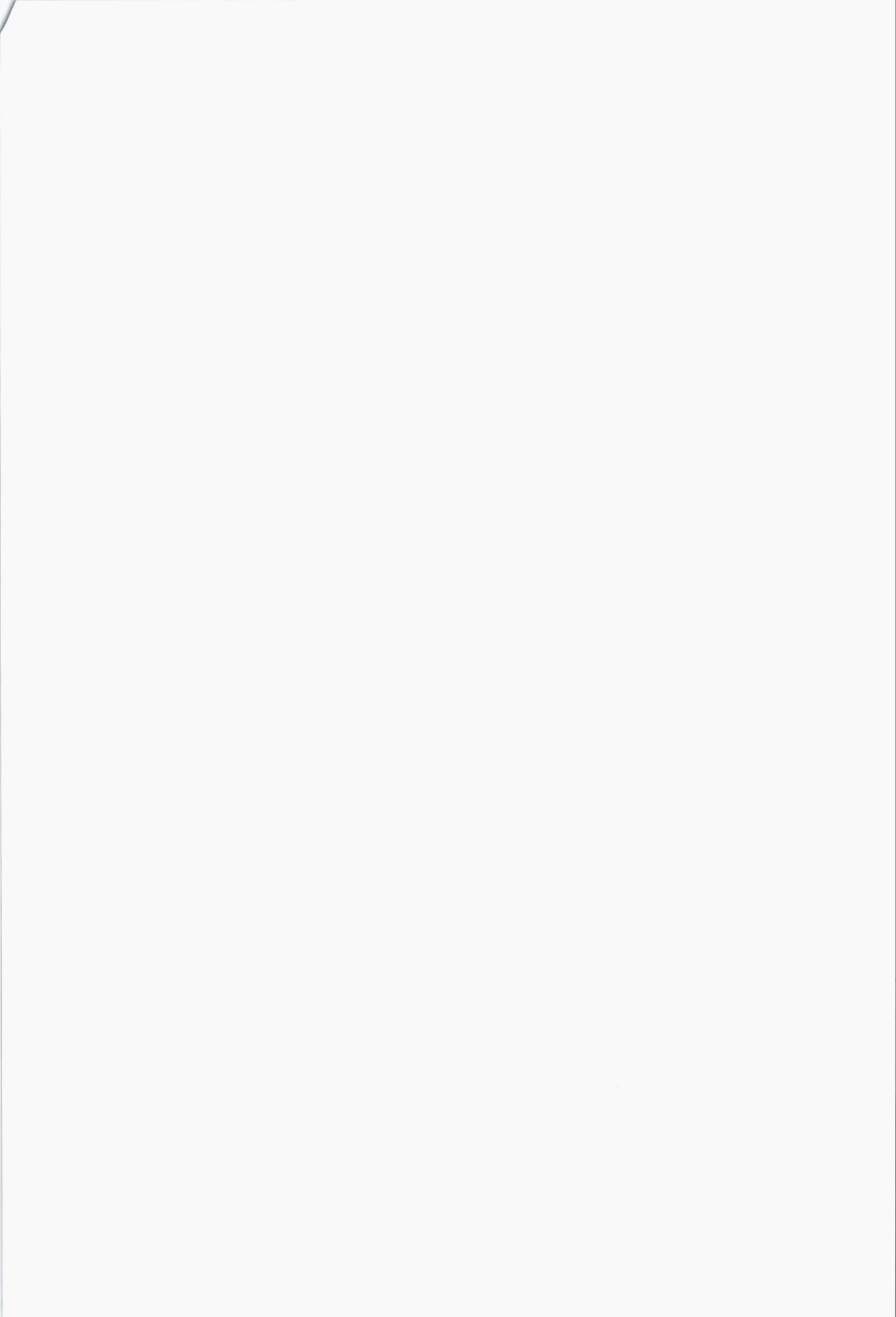
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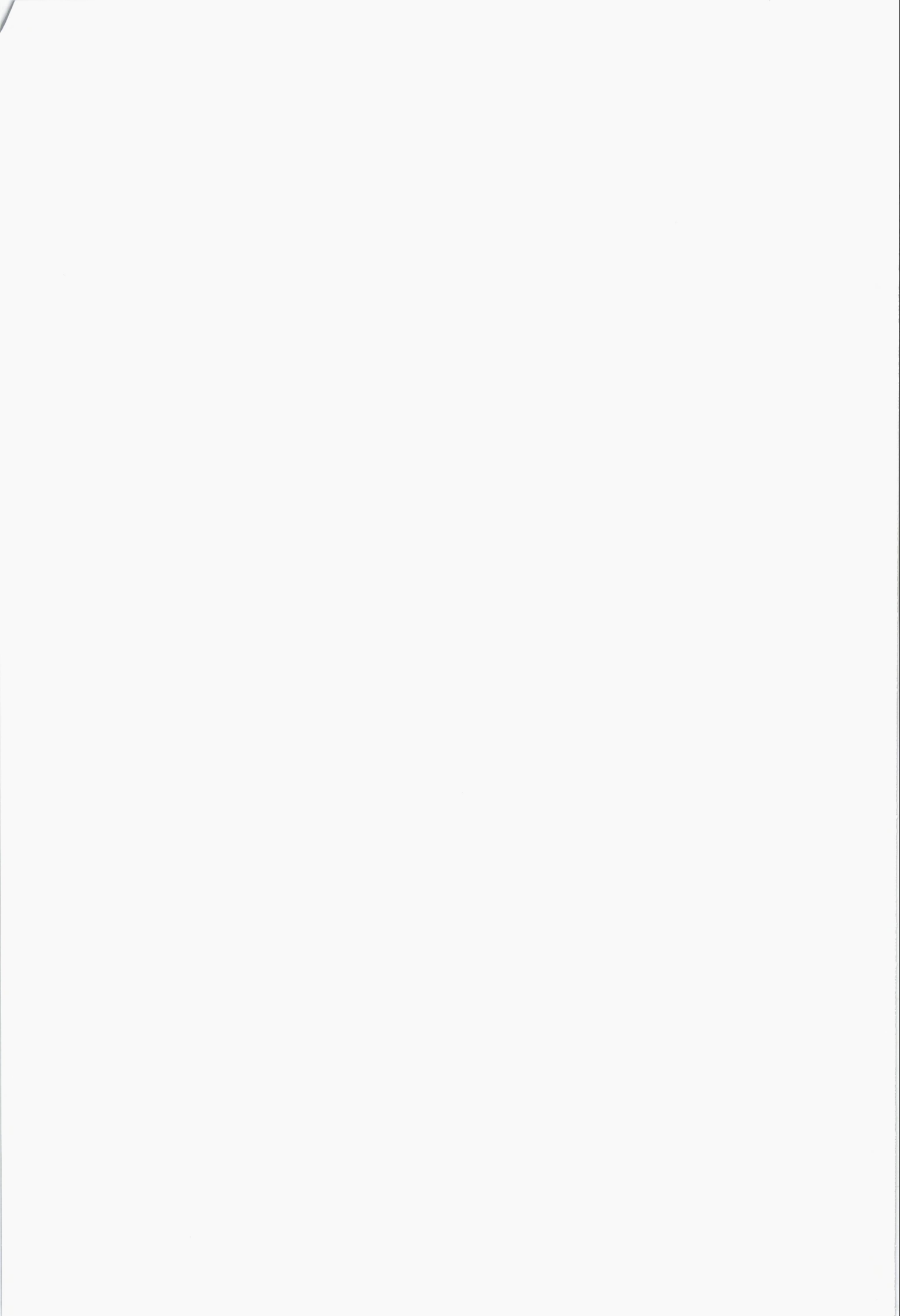
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