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CANNIBALISM AS A STABILISING FACTOR

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Mathematische Modellierung und Simulation

Die mathematisch-naturwissenschaftliche Methode, gegründet auf der Überzeugung, dass „das Buch der Natur in der Sprache der Mathematik geschrieben" sei (Galilei), findet heute weit über ihren ursprünglichen Gegenstandsbereich hinaus Verwendung. *Mathematische Modellierung*, also der Versuch, das Nachdenken über eine Fragestellung in mathematische Termini zu übersetzen, verfolgt den Zweck, sich die Stringenz mathematischer Argumente auch für die Bearbeitung von Problemen außerhalb der Mathematik zu sichern. Im Begriff der *Simulation* ist in diesem Zusammenhang der Anspruch enthalten, dass die Analyse eines mathematischen Modells oder sein Nachvollzug auf dem Computer immer auch auf Erkenntnisse zielt, die über die Mathematik hinausweisen.

Der Erfolg dieser Methode bei der Behandlung physikalischer und technischer Systeme hat es nahegelegt, ihr Anwendungsfeld zu erweitern. In den *Lebens- und Sozialwissenschaften* geht es bis in Bereiche hinein, die gesellschaftliches Handeln zum Gegenstand haben und ihrerseits beeinflussen. Dabei werden häufig nur die wissenschaftlichen Ergebnisse wahrgenommen, während den Methoden, mit denen sie zustandekommen, blind vertraut wird. Doch die Mathematik als „höchste Form der Rationalität" anzupreisen, wie es auch mathematische Fachwissenschaftler gerne tun, besagt noch nichts über ihre Bedeutung für die Erkenntnis gesellschaftlicher und natürlicher Phänomene und Zusammenhänge. Zu hinterfragen ist insbesondere die verbreitete Auffassung, bei mathematischen Modellen handele es sich in aller Schlichtheit um „Abbilder der Wirklichkeit".

Das Zentrum für Modellierung und Simulation und diese Schriftenreihe haben zum Ziel, die *methodischen* Fragestellungen zu behandeln und zu durchleuchten, die die mathematische Bearbeitung „realer" Probleme aufwirft. Die Frage nach dem „richtigen" Einsatz mathematischer Modellierung im Einzelfall gehört ebenso dazu dazu wie die Frage nach Kriterien dafür im Allgemeinen. Gibt es eine „Methode" der Modellierung und Simulation, und worin bestehen ihre Regeln, ihre Möglichkeiten, ihre Grenzen? Es ist klar, dass eine so komplexe Fragestellung mehr als nur einen Zugang erfordert. Gefragt sind u. a.

- Darstellungen und Untersuchungen von selbst entwickelten ebenso wie die Auseinandersetzung mit in der Literatur vorgefundenen mathematischen *Modellklassen* und *Fallstudien*,
- Untersuchungen zu spezifischen, am Modelltyp orientierten *Instrumenten und Methoden* der mathematischen Modellierung,
- *wissenschaftstheoretische und -historische* Abhandlungen zur gesellschaftlichen Bedeutung von Mathematisierungsprozessen.

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Cannibalism as a stabilising factor

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Zusammenfassung

For the niche-model, which is described in the form of nonlinear
differential equations, the influence of cannibalism is researched. It is
shown that inner stable states exist only if the inward-directed pre-
datory intensity is great enough compared with the outward-directed
one. For this model the possibility of *life boat mechanism* is analysed.
Numerical simulations for *Neomysis integer* and *Praunus flexuosus*
show that with the increase of cannibalism in the predator-population
the survival-window grows and the oscillations in the system are sup-
pressed.

Keywords: Niche-model, cannibalism, stability, life boat mechanism.

1 Introduction

Models with structured populations are important in studies of different kinds
of ecosystems, for example see [9,16,21,23]. The reason is that only these
models reveal the often very complex interactions of the populations so that
the influence of these interactions on the dynamic of a single population
and of the whole system can be registered and analysed. In the aggregating
models a great part of the specific information relating to each population,
especially concerning its intraspecific relations, may be lost.

Intraspecific interactions can occur in the form of competition or often of
cannibalism. Cannibalism, once regarded merely as a curious phenomenon,
is now considered to be a significant factor in the structure and dynamic of
many populations. R. Fox [10] and G. A. Polis [22], who contributed substan-
tially to understanding the importance of this mechanism and inspired to

further research, have supplied a good survey of this subject in their publications. Especially cannibalism is wide-spread in marine populations, which are our main field of interest.

The number of works in which cannibalism is researched and modelled is still meagre. W. Gabriel has begun a series of publications on the role of cannibalism as a survival-factor. Since a cannibalistic population bounds itself, cannibalism in a predatory population can lead to preservation of its prey and hence to its own survival. On the other hand, different age stages of this population often have different food sources, so that for the whole population a new access to sources is gained that a non-cannibalistic population otherwise would not have. This phenomenon has often been observed by biologists. In [2] it is modelled and described as the *life boat mechanism*. Thus, cannibalism enables a population to survive when otherwise it may die out. It means that cannibalism plays a stabilising role for the system on the whole. Whether cannibalism is a stabilising factor in an exact mathematical sense is still a question to debate. This problem is the focus of attention in many papers on the subject of cannibalism.

According to [8] cannibalism is a destabilising factor. In [7,17] different results are obtained from different models for *Tribolium castaneum*: Hastings showed that cannibalism has a destabilising effect, whereas Desharnais and Liu indicated a largely stabilising effect of cannibalism. In these models isolated cannibalistic populations which do not clash with others have been studied, and in [8] and [17] the following simplified assumptions have been made. Diekmann et al. substitute the attack-window of the prey stages by a total loss at low age. In Hastings model reproduction in the McKendrick-equation is constant regardless of the size of the stages capable of reproduction. These assumptions may have a crucial influence on the results.

Cushing, [5], showed that different effects may appear in a simple difference-model of cannibalism. They are the *life boat mechanism*, oscillations, chaos. According to [6] the population structure is more responsible than cannibalism for oscillations. Oscillations in predator-prey systems are well known and they have already been described in the classic Lotka-Volterra model, see [18]. The influence of cannibalism on oscillations in such systems has been investigated by Kohlmeier, Ebenhöh [19] and Gabriel et al., [3,4,12]. The results confirm the stabilising effect of cannibalism.

This wide range of results indicates that cannibalism varies in different populations. The fact that the model itself is a significant factor should be taken into consideration as well. Further research into this problem is necessary.

The niche-model of Greve, [14,15], that is represented in the form of system of differential equations, is the basis of our research. This model

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was developed for marine populations and analysed in [20]. The important stabilising role of cannibalism in the system of a single population was shown there. In this paper we consider systems covering more populations. Since the model is very complicated (system of nonlinear differential equations), the analytical approaches require strict simplifications. For this reson, we use appropriate numerical simulations in addition.

2 Stability analysis in systems with several populations

In our research of the niche-model in [20] we dealt mainly with the dynamic of single populations. We noticed that cannibalism in this model is an important factor even under these conditions. It can be the natural cause for the boundedness and the existence of nontrivial stationary points. In the present investigation we considered systems comprising several populations. On comparing the inward-directed predatory intensity with the outward-directed one, we could confirm the stabilising role of cannibalism. These predatory activities affect the system differently, and there is an inner stable point only if cannibalism is large enough.

2.1 Two populations with two stages each

We begin with the case of two populations. Each of them has two age stages, and only the youngest representatives can be attacked by the oldest ones of the two populations. Let x_1, x_2 be the densities of the stages of the first population and x_3, x_4 be the densities of the stages of the second one; x_1 and x_3 correspond to the youngest. The system of differential equations has the form, [20],

$$
\begin{aligned}
x_1' &= -\sigma_{11}x_1 + \sigma_{12}x_2 - f_{12}x_1x_2 - f_{14}x_1x_4 \\
x_2' &= \sigma_{21}x_1 - \sigma_{22}x_2 \\
x_3' &= -\sigma_{33}x_3 + \sigma_{34}x_4 - f_{34}x_3x_4 - f_{32}x_3x_2 \\
x_4' &= \sigma_{43}x_3 - \sigma_{44}x_4.
\end{aligned}
\tag{1}
$$

The coefficients have the following meaning:

σ_{ii} determines the quitting of the i-th age stage (growth and death by starvation),

σ_{ii-1} determines the development from the $(i-1)$-th stage to the i-th,

σ_{12} and σ_{34} determine the reproduction of the youngest stages by the

eldest.

Generally σ_{ij} depend on food suply, [20]. Here we assume that they are constant. The matrices

$$A_1 = \begin{pmatrix} -\sigma_{11} & \sigma_{12} \\ \sigma_{21} & -\sigma_{22} \end{pmatrix}, \quad A_2 = \begin{pmatrix} -\sigma_{33} & \sigma_{34} \\ \sigma_{43} & -\sigma_{44} \end{pmatrix}$$

are called Leslie-matrices of populations, [20].

f_{ij} are constant and determine the intensity of x_j's attacking x_i.

In the stationary point we have

$$x_2 = \frac{\sigma_{21}}{\sigma_{22}} x_1, \qquad x_4 = \frac{\sigma_{43}}{\sigma_{44}} x_3$$

and therefore

$$\begin{aligned} x_1 \{ f_{12} \frac{\sigma_{21}}{\sigma_{22}} x_1 + f_{14} \frac{\sigma_{43}}{\sigma_{44}} x_3 + \Delta_1 \} &= 0 \\ x_3 \{ f_{32} \frac{\sigma_{21}}{\sigma_{22}} x_1 + f_{34} \frac{\sigma_{43}}{\sigma_{44}} x_3 + \Delta_2 \} &= 0, \end{aligned} \tag{2}$$

where

$$\Delta_1 = \frac{1}{\sigma_{22}} \begin{vmatrix} \sigma_{11} & -\sigma_{12} \\ -\sigma_{21} & \sigma_{22} \end{vmatrix}, \quad \Delta_2 = \frac{1}{\sigma_{44}} \begin{vmatrix} \sigma_{33} & -\sigma_{34} \\ -\sigma_{43} & \sigma_{44} \end{vmatrix}.$$

In case $x_1 > 0, x_2 > 0$ it is equal to

$$\begin{aligned} c_{11} x_1 + c_{12} x_3 &= -\Delta_1 \\ c_{21} x_1 + c_{21} x_3 &= -\Delta_2, \end{aligned} \tag{3}$$

where $\quad c_{11} = \dfrac{f_{12}\sigma_{21}}{\sigma_{22}}, \quad c_{12} = \dfrac{f_{14}\sigma_{43}}{\sigma_{44}}, \quad c_{21} = \dfrac{f_{32}\sigma_{21}}{\sigma_{22}}, \quad c_{22} = \dfrac{f_{34}\sigma_{43}}{\sigma_{44}},$

and we see that Δ_1 and Δ_2 must be negative. These are exactly the requirements of instability of origin in systems of single populations, [20].

In case $\Delta \neq 0$ Cramer's rule yields

$$x_1 = \frac{\Delta_{x_1}}{\Delta}, \quad x_3 = \frac{\Delta_{x_3}}{\Delta}, \quad \Delta_{x_1} = \begin{vmatrix} -\Delta_1 & c_{12} \\ -\Delta_2 & c_{22} \end{vmatrix}, \quad \Delta_{x_3} = \begin{vmatrix} c_{12} & -\Delta_1 \\ c_{21} & -\Delta_2 \end{vmatrix},$$

$$\Delta = \begin{vmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{vmatrix} = \frac{\sigma_{21}\sigma_{43}}{\sigma_{22}\sigma_{44}} \Delta_f, \quad \Delta_f = \begin{vmatrix} f_{12} & f_{14} \\ f_{32} & f_{34} \end{vmatrix}. \tag{4}$$

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Since x_1 and x_2 are positive, Δ_{x_1}, Δ_{x_2} and Δ must have the same signs. From (4) it follows that Δ_f has the same sign as well.

We examined the stability in the stationary point in case $x_1 > 0$, $x_2 > 0$. For that purpose we considered the following characteristic polynomial $P = P(\lambda)$

$$\begin{vmatrix} \sigma_{11} + f_{12}x_2 + f_{14}x_4 + \lambda & f_{12}x_1 - \sigma_{12} & 0 & f_{14}x_1 \\ -\sigma_{21} & \sigma_{22} + \lambda & 0 & 0 \\ 0 & f_{32}x_3 & \sigma_{33} + f_{32}x_2 + f_{34}x_4 + \lambda & f_{34}x_3 - \sigma_{34} \\ 0 & 0 & -\sigma_{43} & \sigma_{44} + \lambda \end{vmatrix}.$$

By expanding this determinant according to the first two columns, we obtained

$$P(\lambda) = d_{11}(\lambda)d_{22}(\lambda) - d_{21}(\lambda)d_{12}(\lambda), \tag{5}$$

where

$$d_{11} = d_{11}(\lambda) = \begin{vmatrix} \sigma_{11} + f_{12}x_2 + f_{14}x_4 + \lambda & -\sigma_{12} + f_{12}x_1 \\ -\sigma_{21} & \sigma_{22} + \lambda \end{vmatrix},$$

$$d_{22}(\lambda) = \begin{vmatrix} \sigma_{33} + f_{32}x_2 + f_{34}x_3 + \lambda & -\sigma_{34} + f_{34}x_3 \\ -\sigma_{43} & \sigma_{44} + \lambda \end{vmatrix},$$

$$d_{21}(\lambda) = \begin{vmatrix} 0 & f_{32}x_3 \\ -\sigma_{21} & \sigma_{22} + \lambda \end{vmatrix}, \quad d_{22}(\lambda) = \begin{vmatrix} 0 & f_{14}x_1 \\ -\sigma_{43} & \sigma_{44} + \lambda \end{vmatrix}.$$

From $f_{12}x_2 + f_{14}x_4 = -\Delta_1$ and $f_{32}x_2 + f_{34}x_3 = -\Delta_2$ it follows that for an inner stationary point it satisfies

$$\begin{aligned} d_{11} &= \lambda^2 + \lambda T_1 + r_1, \quad T_1 = \sigma_{22} + \frac{\sigma_{12}\sigma_{21}}{\sigma_{22}} > 0, \quad r_1 = f_{12}\sigma_{21}x_1 > 0, \\ d_{22} &= \lambda^2 + \lambda T_2 + r_2, \quad T_2 = \sigma_{44} + \frac{\sigma_{34}\sigma_{43}}{\sigma_{44}} > 0, \quad r_2 = f_{12}\sigma_{21}x_1, \tag{6} \\ d_{21} &= \sigma_{21}f_{32}x_3, \quad d_{12} = \sigma_{43}f_{14}x_1. \end{aligned}$$

Thus, we have for the characteristic polynomial in the inner stationary point

$$\begin{aligned} P &= \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = \\ &\quad (\lambda^2 + \lambda T_1 + r_1)(\lambda^2 + \lambda T_2 + r_2) - f_{12}\sigma_{21}x_1 f_{34}\sigma_{43}x_3, \\ &\quad a_1 = T_1 + T_2, \quad a_2 = T_1 T_2 + r_1 + r_2, \quad a_3 = T_1 r_2 + T_2 r_1, \tag{7} \\ &\quad a_4 = r_1 r_2 - f_{14}\sigma_{21}x_1 f_{32}\sigma_{43}x_3 = \Delta_f \sigma_{21}\sigma_{43}x_1 x_3. \end{aligned}$$

The stationary point is asymptotically stable if the real parts of all the roots of the characteristic polynomial are negative and it is unstable if at least one of the roots has a positive real part, [1]. According to the Routh-Hurwitz criterion, [13], the real parts of the roots of the polynomial $P = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4$ are negative if and only if

$$a_1 > 0, \quad a_1a_2 > a_3, \quad a_3(a_1a_2 - a_3) > a_1^2a_4, \quad a_4 > 0.$$

Due to (6,7) it is obvious that the first three inequalities hold. In fact, we have $a_1 = T_1 + T_2 > 0$ and $a_1a_2 = (T_1 + T_2)(T_1T_2 + r_1 + r_2) > T_1r_2 + T_2r_1 = a_3$. The third inequality is fulfilled, because

$$
\begin{aligned}
a_3(a_1a_2 - a_3) &= (T_1r_2 + T_2r_1)(T_1^2T_2 + T_1r_1 + T_1T_2^2 + T_2r_2) \\
&> T_1^2r_1r_2 + T_2^2r_1r_2 + T_1T_2(r_1^2 + r_2^2) \geq (T_1 + T_2)^2)r_1r_2 \\
&= a_1^2 f_{12}f_{34}\sigma_{21}\sigma_{43}x_1x_3 > a_1^2\Delta_f\sigma_{21}\sigma_{43}x_1x_3 = a_1^2a_4.
\end{aligned}
$$

According to (7), a_4 and Δ_f have the same signs. Hence, the stationary point is asymptotically stable at $\Delta_f > 0$ and it is unstable at $\Delta_f < 0$.

If linear system (3) has solutions at $\Delta_f = 0$, they form a line segment and, evidently, they are not stable. In this case, due to (7), we have $a_4 = 0$ and $P = \lambda(\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3)$. It is remarkable that here is a root equal to 0, and the real parts of the others are negative. By means of the Routh-Hurwitz criterion we see again for the polynomial $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$

$$a_1 > 0, \quad a_1a_2 > a_3, \quad a_3 > 0.$$

Thus, the asymptotic stability is equivalent to $\Delta_f > 0$, i.e. $\Delta > 0$, $\Delta_{x_1} > 0$ and $\Delta_{x_3} > 0$. From $\Delta_1 < 0$, $\Delta_2 < 0$ it follows that the last two conditions yield

$$f_{12} > \frac{|\Delta_1|}{|\Delta_2|}f_{32}, \quad f_{34} > \frac{|\Delta_2|}{|\Delta_1|}f_{14}. \tag{8}$$

That means that the inward-directed predatory intensity must be great enough compared with the outward-directed one. On the other hand, (8) simply leads to $\Delta_f > 0$. Hence, $\Delta > 0$ holds and Cramer's rule results in a nontrivial solution of the system (3) in case $\Delta_1 < 0$ and $\Delta_2 < 0$. Therefore, we have an inner asymptotically stable stationary point. Thus, we come to the following result.

Theorem 1. *System (1) with constant Leslie-matrices has an inner asymptotically stable stationary point if and only if*

$$\Delta_1 = \frac{1}{\sigma_{22}}\begin{vmatrix} \sigma_{11} & -\sigma_{12} \\ -\sigma_{21} & \sigma_{22} \end{vmatrix} < 0, \quad \Delta_2 = \frac{1}{\sigma_{44}}\begin{vmatrix} \sigma_{33} & -\sigma_{34} \\ -\sigma_{43} & \sigma_{44} \end{vmatrix} < 0$$

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$$\text{and} \qquad f_{12} > \frac{|\Delta_1|}{|\Delta_2|} f_{32}, \quad f_{34} > \frac{|\Delta_2|}{|\Delta_1|} f_{14}.$$

2.2 Two populations with several stages

We will generalise this theorem partly for systems of several populations and age stages as well. Since the complete analysis is generally too complicated, only necessary conditions of stability can be found. Here we consider a system of two populations with n and k age stages, where only the youngest representatives are attacked. The system of differential equations for the densities $x_1, \cdots, x_{n+k}$ of the age stages of these populations has the form

$$
\begin{aligned}
x_1' &= -\sigma_{11}x_1 + \sigma_{12}x_2 + \cdots + \sigma_{1n}x_n - \sum_{j=1}^{n+k} f_{1j}x_1x_j \\
x_2' &= \sigma_{21}x_1 - \sigma_{22}x_2 \\
&\vdots \\
x_n' &= \sigma_{nn-1}x_{n-1} - \sigma_{nn}x_n. \\
x_{n+1}' &= -\sigma_{n+1n+1}x_{n+1} + \sigma_{n+1n+2}x_{n+2} + \cdots + \sigma_{n+1n+k}x_{n+k} - \sum_{j=1}^{n+k} f_{n+1j}x_{n+1}x_j \\
x_{n+2}' &= \sigma_{n+2n+1}x_{n+1} - \sigma_{n+2n+2}x_{n+2} \\
&\vdots \\
x_{n+k}' &= \sigma_{n+kn+k-1}x_{n+k-1} - \sigma_{n+kn+k}x_{n+k}.
\end{aligned}
$$

We assume again that σ_{ij} are constant. Here f_{11} and f_{n+1n+1} equal 0, but it is insignificant for the following.

Let $p = n + 1$, $q = n + k$, and analogous to the preceding

$$\Delta_1 = \frac{1}{\sigma_{22} \cdots \sigma_{nn}} \begin{vmatrix} \sigma_{11} & -\sigma_{12} & -\sigma_{13} & \cdots & -\sigma_{1n} \\ -\sigma_{21} & \sigma_{22} & 0 & \cdots & 0 \\ 0 & -\sigma_{32} & \sigma_{33} & \cdots & 0 \\ \vdots & & & \ddots & \\ 0 & \cdots & 0 & -\sigma_{nn-1} & \sigma_{nn} \end{vmatrix},$$

$$\Delta_2 = \frac{1}{\sigma_{n+2n+2} \cdots \sigma_{qq}} \begin{vmatrix} \sigma_{pp} & -\sigma_{pp+1} & -\sigma_{pp+2} & \cdots & -\sigma_{pq} \\ -\sigma_{n+2p} & \sigma_{n+2n+2} & 0 & \cdots & 0 \\ 0 & -\sigma_{n+3n+2} & \sigma_{n+3n+3} & \cdots & 0 \\ \vdots & & & \ddots & \\ 0 & \cdots & 0 & -\sigma_{qq-1} & \sigma_{qq} \end{vmatrix}.$$

The following determinants c_{11}, c_{12}, c_{21} and c_{22} arise after the evident substitution of the first rows in Δ_1 and Δ_2. These determinants are not negative.

$$c_{11} = \frac{1}{\sigma_{22} \cdots \sigma_{nn}} \begin{vmatrix} 0 & f_{12} & f_{13} & \cdots & f_{1n} \\ -\sigma_{21} & \sigma_{22} & 0 & \cdots & 0 \\ 0 & -\sigma_{32} & \sigma_{33} & \cdots & 0 \\ \vdots & & & \ddots & \\ 0 & \cdots & 0 & -\sigma_{nn-1} & \sigma_{nn} \end{vmatrix},$$

$$c_{21} = \frac{1}{\sigma_{22} \cdots \sigma_{nn}} \begin{vmatrix} f_{n+11} & f_{n+12} & f_{n+13} & \cdots & f_{n+1n} \\ -\sigma_{21} & \sigma_{22} & 0 & \cdots & 0 \\ 0 & -\sigma_{32} & \sigma_{33} & \cdots & 0 \\ \vdots & & & \ddots & \\ 0 & \cdots & 0 & -\sigma_{nn-1} & \sigma_{nn} \end{vmatrix},$$

$$c_{12} = \frac{1}{\sigma_{n+2n+2} \cdots \sigma_{n+kn+k}} \begin{vmatrix} f_{1n+1} & f_{1n+2} & \cdots & f_{1n+k} \\ -\sigma_{n+2n+1} & \sigma_{n+2n+2} & \cdots & 0 \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{n+kn+k-1} & \sigma_{n+kn+k} \end{vmatrix},$$

$$c_{22} = \frac{1}{\sigma_{n+2n+2} \cdots \sigma_{n+kn+k}} \begin{vmatrix} 0 & f_{n+1n+2} & \cdots & f_{n+1n+k} \\ -\sigma_{n+2n+1} & \sigma_{n+2n+2} & \cdots & 0 \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{n+kn+k-1} & \sigma_{n+kn+k} \end{vmatrix}.$$

In the stationary point we have

$$x_2 = \frac{\sigma_{21}}{\sigma_{22}} x_1, \cdots, x_n = \frac{\sigma_{nn-1} \cdots \sigma_{21}}{\sigma_{nn} \cdots \sigma_{22}} x_1,$$

$$x_{n+2} = \frac{\sigma_{n+2n+1}}{\sigma_{n+2n+2}} x_{n+1}, \cdots, x_{n+k} = \frac{\sigma_{n+kn+k-1} \cdots \sigma_{n+2n+1}}{\sigma_{n+kn+k} \cdots \sigma_{n+2n+2}} x_{n+1}$$

and the substitution leads to the following system for x_1 and x_{n+1}

$$\begin{aligned} x_1\{c_{11}x_1 + c_{12}x_{n+1} + \Delta_1\} &= 0 \\ x_{n+1}\{c_{21}x_1 + c_{22}x_{n+1} + \Delta_2\} &= 0. \end{aligned}$$

When $x_1 \neq 0$, $x_{n+1} \neq 0$ we have the linear system

$$\begin{aligned} c_{11}x_1 + c_{12}x_{n+1} &= -\Delta_1 \\ c_{21}x_1 + c_{22}x_{n+1} &= -\Delta_2, \end{aligned}$$

whereby Δ_1 and Δ_2 must be negative.

Let

$$\Delta = \begin{vmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{vmatrix}, \quad \Delta_{x_1} = \begin{vmatrix} -\Delta_1 & c_{12} \\ -\Delta_2 & c_{22} \end{vmatrix}, \quad \Delta_{x_{n+1}} = \begin{vmatrix} c_{11} & -\Delta_1 \\ c_{21} & -\Delta_2 \end{vmatrix}.$$

Then in case $\Delta \neq 0$ we obtain

$$x_1 = \frac{\Delta_{x_1}}{\Delta}, \quad x_{n+1} = \frac{\Delta_{x_{n+1}}}{\Delta}.$$

Hence, we see that Δ, Δ_{x_1} and $\Delta_{x_{n+1}}$ have the same signs.

Suppose $D_{11} = D_{11}(\lambda)$ und $D_{22} = D_{22}(\lambda)$ the following matrices

$$D_{11} = \begin{pmatrix} \sigma_{11} + \sum_{j=1}^{n+k} f_{1j}x_j + \lambda & -\sigma_{12} + f_{12}x_1 & \cdots & -\sigma_{1n} + f_{1n}x_1 \\ -\sigma_{21} & \sigma_{22} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{nn-1} & \sigma_{nn} + \lambda \end{pmatrix},$$

$$D_{22} = \begin{pmatrix} \sigma_{pp} + \sum_{j=1}^{n+k} f_{n+1j}x_j + \lambda & -\sigma_{pp+1} + f_{pp+1}x_p & \cdots & -\sigma_{pq} + f_{pq}x_p \\ -\sigma_{p+1p} & \sigma_{p+1p+1} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{qq-1} & \sigma_{qq} + \lambda \end{pmatrix}$$

and $d_{11}(\lambda) = det D_{11}(\lambda)$, $d_{22}(\lambda) = det D_{22}(\lambda)$ denote their determinants. We obtain the following determinants by substituting the first rows in D_{11} and D_{22} respectively

$$d_{21}(\lambda) = \begin{vmatrix} f_{n+11}x_{n+1} & f_{n+12}x_{n+1} & \cdots & f_{n+1n}x_{n+1} \\ -\sigma_{21} & \sigma_{22} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{nn-1} & \sigma_{nn} + \lambda \end{vmatrix},$$

$$d_{12}(\lambda) = \begin{vmatrix} f_{1n+1}x_1 & f_{1n+2}x_1 & \cdots & f_{1n+k}x_1 \\ -\sigma_{p+1p} & \sigma_{p+1p+1} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{qq-1} & \sigma_{qq} + \lambda \end{vmatrix}.$$

Particularly,

$$d_{21}(0) = x_{n+1}\sigma_{22} \cdots \sigma_{nn} c_{21}, \quad d_{12}(0) = x_1 \sigma_{n+2n+2} \cdots \sigma_{n+kn+k} c_{12}.$$

In order to be sure that the coefficient at λ^{n+k} equals 1, we always use $Q = (-1)^{n+k}P(\lambda)$ instead of the characteristic polynomial $P(\lambda)$,

$$Q = \begin{vmatrix} & & & f_{1n+1}x_1 & \cdots & f_{1n+k}x_1 \\ & D_{11}(\lambda) & & 0 & \cdots & 0 \\ & & & & \vdots & \\ & & & 0 & \cdots & 0 \\ f_{n+11}x_{n+1} & \cdots & f_{n+1n}x_{n+1} & & & \\ & \cdots & 0 & & & \\ & \vdots & & & D_{22}(\lambda) & \\ 0 & \cdots & 0 & & & \end{vmatrix}.$$

By expanding the determinant Q according to the first n columns we should take into consideration only two of the determinants: with the rows from 1 to n and with the rows from 2 to $n + 1$. Otherwise there is a zero-row either in the matrix with the n first columns or in its adjoint submatrix. The determinant with the rows from 2 to $n + 1$ apparently equals $(-1)^{n-1}d_{21}$. Thus, we obtain

$$Q(\lambda) = sg_1 \cdot d_{11}(\lambda)d_{22}(\lambda) + sg_2 \cdot d_{12}(\lambda)d_{21}(\lambda),$$

where $sg_1 = (-1)^{1+\cdots+n+1+\cdots+n} = 1$, $sg_2 = (-1)^{1+\cdots+n+2\cdots+n+1}(-1)^{n-1} = -1$. So it holds

$$Q(\lambda) = \lambda^n + a_1\lambda^{n-1} + \cdots + a_n = d_{11}(\lambda)d_{22}(\lambda) - d_{12}(\lambda)d_{21}(\lambda)$$

and a_n is equal to

$$a_n = Q(0) = d_{11}(0)d_{22}(0) - x_1x_{n+1}c_{12}c_{21}\sigma_{22}\cdots\sigma_{nn}\sigma_{n+2n+2}\cdots\sigma_{n+kn+k}.$$

In the inner stationary point the following condition $\sum_{j=1}^{m+k} f_{1j}x_j = -\Delta_1$ holds and by expanding $d_{11}(0)$ according to the first row we obtain

$$d_{11}(0) = \Delta_1\sigma_{22}\cdots\sigma_{nn} - \Delta_1\sigma_{22}\cdots\sigma_{nn} + x_1c_{11}\sigma_{22}\cdots\sigma_{nn} = c_{11}x_1\sigma_{22}\cdots\sigma_{nn}.$$

Analog $d_{22}(0) = c_{22}x_{n+1}\sigma_{n+2n+2}\cdots\sigma_{n+kn+k}$. Finally, we come to

$$\begin{aligned} a_n &= \{c_{11}c_{22} - c_{12}c_{21}\}x_1x_{n+1}\sigma_{22}\cdots\sigma_{nn}\sigma_{n+2n+2}\cdots\sigma_{n+kn+k} \\ &= x_1x_{n+1}\Delta\sigma_{22}\cdots\sigma_{nn}\sigma_{n+2n+2}\cdots\sigma_{n+kn+k}, \end{aligned}$$

so that a_n and Δ have the same signs. The condition $a_n > 0$ is necessary for the positivity of the real parts of the roots of $Q(\lambda)$. This is equivalent to $\Delta > 0$, and hence $\Delta_{x_1} > 0$ and $\Delta_{x_{n+1}} > 0$. Immediately we come to

$$\Delta_1 < 0, \quad \Delta_2 < 0, \quad c_{11} > \frac{|\Delta_1|}{|\Delta_2|}c_{21}, \quad c_{22} > \frac{|\Delta_2|}{|\Delta_1|}c_{12}.$$

The last two inequalities indicate that for the existence of an inner asymptotically stable point the inward-directed predatory intensity must be great enough compared with the outward-directed one. The inequality $\Delta > 0$ follows automatically.

2.3 Several populations

We now turn to the case of several populations in which also only the youngest age stages are attacked. Let m be the number of the populations and $n_i, 1 \leq i \leq m$, the number of the age stages of the $i-$th population. For the sake of brevity, $q = n_1 + \cdots + n_m$ denotes the total number of all the age stages, p_i and q_i denote the numbers of the youngest and the oldest age stage of the $i-$th population, $(p_i = n_1 + \cdots + n_{i-1} + 1, \; q_i = n_1 + \cdots + n_i)$, and $r_i = p_i + 1$ as well. We also call y_i the density of the youngest stage of the $i-$th population, so that $y_i = x_{p_i}$. The system of differential equations consists of m blocks, which correspond to the populations. The $i-$th block, $1 \leq i \leq m$, is the following

$$
\begin{aligned}
x'_{p_i} &= -\sigma_{p_i p_i} x_{p_i} + \sum_{j=r_i}^{q_i} \sigma_{p_i j} x_j - x_{p_i} \left(\sum_{k=1}^{q} f_{p_i k} x_k \right) \\
x'_{r_i} &= \sigma_{r_i p_i} x_{p_i} - \sigma_{r_i r_i} x_{r_i} \\
&\;\;\vdots \\
x'_{q_i} &= \sigma_{q_i q_i - 1} x_{q_i - 1} - \sigma_{q_i q_i} x_{q_i}
\end{aligned}
$$

For $1 \leq i \leq m$ let $\quad \nu_i = \sigma_{p_i+1 p_i+1} \cdots \sigma_{q_i q_i},$

$$
\Delta_i = \frac{1}{\nu_i}
\begin{vmatrix}
\sigma_{p_i p_i} & -\sigma_{p_i r_i} & -\sigma_{p_i p_i+2} & \cdots & -\sigma_{p_i q_i} \\
-\sigma_{r_i p_i} & \sigma_{r_i r_i} & 0 & \cdots & 0 \\
0 & -\sigma_{p_i+2 r_i} & \sigma_{p_i+2 p_i+2} & 0 & \cdots \\
\vdots & & & \ddots & \\
0 & \cdots & 0 & -\sigma_{q_i q_i - 1} & \sigma_{q_i q_i}
\end{vmatrix}
$$

and for $1 \leq i \leq m$, $1 \leq j \leq m$

$$
c_{ji} = \frac{1}{\nu_i}
\begin{vmatrix}
f_{p_j p_i} & f_{p_j r_i} & f_{p_j p_i+2} & \cdots & f_{p_j q_i} \\
-\sigma_{r_i p_i} & \sigma_{r_i r_i} & 0 & \cdots & 0 \\
0 & -\sigma_{p_i+2 r_i} & \sigma_{p_i+2 p_i+2} & 0 & \cdots \\
\vdots & & & \ddots & \\
0 & \cdots & 0 & -\sigma_{q_i q_i - 1} & \sigma_{q_i q_i}
\end{vmatrix}.
$$

All c_{ji} are not negative. We assume that the coefficients σ_{ij} are constant and for each j not all c_{ji} equal 0. The latter condition means that each population is attacked. In the stationary point we have again

$$x_{r_i} = \frac{\sigma_{r_i p_i}}{\sigma_{r_i r_i}} y_i, \cdots, x_{q_i} = \frac{\sigma_{r_i p_i} \cdots \sigma_{q_i q_i - 1}}{\sigma_{r_i r_i} \cdots \sigma_{q_i q_i}} y_i, \quad 1 \le i \le m, \tag{9}$$

and after substitutions the first equations of the blocks can be simply transformed into the following system

$$y_1 \{ c_{11} y_1 + \cdots + c_{1m} y_m + \Delta_1 \} = 0$$
$$\vdots$$
$$y_m \{ c_{m1} y_1 + \cdots + c_{mm} y_m + \Delta_m \} = 0.$$

Particularly, for an inner stationary point $y_i > 0$ for $1 \le i \le m$. Thus, we obtain the linear system as follows

$$c_{11} y_1 + \cdots + c_{1m} y_m = -\Delta_1$$
$$\vdots \tag{10}$$
$$c_{m1} y_1 + \cdots + c_{mm} y_m = -\Delta_m$$

and all the determinants $\Delta_1, \cdots, \Delta_m$ are negative if an inner stationary point exists.

On the other hand, let

$$\Delta = \begin{vmatrix} c_{11} & \cdots & c_{1m} \\ & \vdots & \\ c_{m1} & \cdots & c_{mm} \end{vmatrix} \neq 0, \quad \Delta_{y_i} = \begin{vmatrix} c_{1m} & \cdots & -\Delta_1 & \cdots & c_{1m} \\ & & \vdots & & \\ c_{m1} & \cdots & -\Delta_m & \cdots & c_{mm} \end{vmatrix}$$

be the determinants of the system (10) and the determinants for $y_i, 1 \le i \le m$, in Cramer's rule. Then $y_i = \Delta_{y_i} / \Delta$ holds, and therefore $\Delta, \Delta_{y_1}, \cdots, \Delta_{y_m}$ have the same signs if an inner stationary point exists.

Let $P(\lambda)$ be the characteristic polynomial and $Q(\lambda) = (-1)^q P(\lambda)$. The $q \times q-$matrix for Q consists of blocks

$$Q = \begin{vmatrix} D_{11} & \cdots & D_{1m} \\ & \vdots & \\ D_{m1} & \cdots & D_{mm} \end{vmatrix},$$

$$D_{ii} = \begin{pmatrix} \sigma_{p_i p_i} + \sum_{k=1}^{q} f_{p_i k} x_k + \lambda & -\sigma_{p_i r_i} + f_{p_i r_i} y_i & \cdots & -\sigma_{p_i q_i} + f_{p_i q_i} y_i \\ -\sigma_{r_i p_i} & \sigma_{r_i r_i} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{q_i q_i - 1} & \sigma_{q_i q_i} + \lambda \end{pmatrix},$$

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$$D_{ij} = \begin{pmatrix} f_{p_i p_j} y_i & \cdots & f_{p_i q_j} y_i \\ 0 & \cdots & 0 \\ & \vdots & \\ 0 & \cdots & 0 \end{pmatrix} \quad \text{for } i \neq j.$$

By expanding Q according to the m rows with the numbers $p_1 = 1, \cdots, p_m$ or by induction on the number m of populations (for instance by expanding the determinant according to the first n_1 columns at the step of the induction) we obtain the following equality

$$Q(\lambda) = \begin{vmatrix} d_{11}(\lambda) & \cdots & d_{1m}(\lambda) \\ & \vdots & \\ d_{m1}(\lambda) & \cdots & d_{mm}(\lambda) \end{vmatrix},$$

where the elements $d_{ij} = d_{ij}(\lambda)$ equal

$$d_{ii} = \det D_{ii}, \quad d_{ij} = \begin{vmatrix} f_{p_i p_j} y_i & f_{p_i r_j} y_i & \cdots & f_{p_i q_j} y_i \\ -\sigma_{r_j p_j} & \sigma_{r_j r_j} + \lambda & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{q_j q_j - 1} & \sigma_{q_j q_j} + \lambda \end{vmatrix} \quad \text{for } i \neq j.$$

At $i \neq j$ we immediately see that $d_{ij}(0) = \nu_i y_i c_{ij}$ and in the inner stationary point in consideration of $\sum_{k=1}^{q} f_{p_i k} x_k = -\Delta_i$ we obtain

$$d_{ii}(0) = \nu_i \{ \Delta_i + \sum_{k=1}^{q} f_{p_i k} x_k + c_{ii} y_i \} = \nu_i y_i c_{ii}.$$

Thus,

$$Q(0) = \nu_1 y_1 \cdots \nu_m y_m \begin{vmatrix} c_{11} & \cdots & c_{1m} \\ & \vdots & \\ c_{m1} & \cdots & c_{mm} \end{vmatrix} = \nu_1 y_1 \cdots \nu_m y_m \Delta.$$

The condition $Q(0) > 0$ is necessary for the negativity of the real parts of all the eigenvalues, i. e. for the asymptotic stability. All ν_i are positive, y_i are also positive for an inner point in the state space. Thus, $\Delta > 0$ is necessary for the existence of an asymptotically stable inner point. Since Δ_{y_i} and Δ have the same signs, we obtain the following necessary condition of the existence of an inner asymptotically stable point

$$\Delta > 0, \quad \Delta_i < 0, \quad \Delta_{y_i} > 0 \text{ for } 1 \leq i \leq m.$$

The conditions $\Delta_i < 0$, $1 \leq i \leq m$, are necessary for the instability of origins for single populations (which do not necessarily die out), see [20]. The inequalities $\Delta_{y_i} > 0$ are restrictions of the predatory intensities.

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2.4 Other directions of predatory intensities

Now we also will show the stabilising effect of cannibalism for the systems in which the predatory intensities focus on the middle age stages. We confine ourselves to the case of two populations. Each of the populations has three age stages. To avoid applying unwieldy terms, we assume that only the oldest stages are predators on the middle ones. The system of differential equations has the form

$$
\begin{aligned}
x_1' &= -\sigma_{11}x_1 + \sigma_{12}x_2 + \sigma_{13}x_3 \\
x_2' &= \sigma_{21}x_1 - \sigma_{22}x_2 - x_2\{f_{23}x_3 + f_{26}x_6\} \\
x_3' &= \sigma_{32}x_2 - \sigma_{33}x_3 \\
x_4' &= -\sigma_{44}x_4 + \sigma_{45}x_5 + \sigma_{46}x_6 \\
x_5' &= \sigma_{54}x_4 - \sigma_{55}x_5 - x_5\{f_{53}x_3 + f_{56}x_6\} \\
x_6' &= \sigma_{65}x_5 - \sigma_{66}x_6
\end{aligned}
\tag{11}
$$

x_1, x_2, x_3 are the age stages of the first population, x_4, x_5, x_6 - of the second one. The coefficients σ_{ij} and f_{ij} are constant. In the stationary point we have

$$
x_3 = \frac{\sigma_{32}}{\sigma_{33}}x_2, \ \ x_1 = \frac{\sigma_{12}}{\sigma_{11}}x_2 + \frac{\sigma_{13}}{\sigma_{11}}x_3 = \left(\frac{\sigma_{12}}{\sigma_{11}} + \frac{\sigma_{13}\sigma_{32}}{\sigma_{11}\sigma_{33}}\right)x_2,
$$
$$
x_6 = \frac{\sigma_{65}}{\sigma_{66}}x_5, \ \ x_4 = \frac{\sigma_{45}}{\sigma_{44}}x_5 + \frac{\sigma_{46}}{\sigma_{44}}x_6 = \left(\frac{\sigma_{45}}{\sigma_{44}} + \frac{\sigma_{46}\sigma_{65}}{\sigma_{44}\sigma_{66}}\right)x_5.
$$

It is clear that for the coordinates $x_3 \neq 0$ and $x_6 \neq 0$ at an inner stationary point we obtain the following linear system

$$
\begin{aligned}
f_{23}x_3 + f_{26}x_6 &= -\Delta_1 \\
f_{53}x_3 + f_{56}x_6 &= -\Delta_2 \quad,
\end{aligned}
\tag{12}
$$

where

$$
\Delta_1 = \frac{1}{\sigma_{11}\sigma_{33}}\begin{vmatrix} \sigma_{11} & -\sigma_{12} & -\sigma_{13} \\ -\sigma_{21} & \sigma_{22} & 0 \\ 0 & -\sigma_{32} & \sigma_{33} \end{vmatrix}, \quad \Delta_2 = \frac{1}{\sigma_{44}\sigma_{66}}\begin{vmatrix} \sigma_{44} & -\sigma_{45} & -\sigma_{46} \\ -\sigma_{54} & \sigma_{55} & 0 \\ 0 & -\sigma_{65} & \sigma_{66} \end{vmatrix}.
$$

$\Delta_1 < 0$ and $\Delta_2 < 0$ are necessary for $x_3 > 0$, $x_6 > 0$. They are the conditions of instability for the trivial solutions of single populations again. Let

$$
\Delta_f = \begin{vmatrix} f_{23} & f_{26} \\ f_{53} & f_{56} \end{vmatrix}, \quad \Delta_{x_3} = \begin{vmatrix} -\Delta_1 & f_{26} \\ -\Delta_2 & f_{56} \end{vmatrix}, \quad \Delta_{x_6} = \begin{vmatrix} f_{23} & -\Delta_1 \\ f_{53} & -\Delta_2 \end{vmatrix}.
\tag{13}
$$

Then in case $\Delta_f \neq 0$ we have

$$
x_3 = \frac{\Delta_{x_3}}{\Delta_f}, \quad x_6 = \frac{\Delta_{x_6}}{\Delta_f},
$$

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so that Δ_f, Δ_{x_3} and Δ_{x_6} have the same signs. The matrix of the linearized system is

$$
A = \begin{pmatrix}
-\sigma_{11} & \sigma_{12} & \sigma_{13} & 0 & 0 & 0 \\
\sigma_{21} & -\sigma_{22} - \sum_j f_{2j}x_j & -f_{23}x_2 & 0 & 0 & -f_{26}x_2 \\
0 & \sigma_{32} & -\sigma_{33} & 0 & 0 & 0 \\
0 & 0 & 0 & -\sigma_{44} & \sigma_{45} & \sigma_{46} \\
0 & 0 & -f_{53}x_5 & \sigma_{54} & -\sigma_{55} - \sum_j f_{5j}x_j & -f_{56}x_5 \\
0 & 0 & 0 & 0 & \sigma_{65} & -\sigma_{66}
\end{pmatrix}.
$$

From (12) it follows that the characteristic polynomial has the form

$$
P(\lambda) = \begin{vmatrix}
\lambda + \sigma_{11} & -\sigma_{12} & -\sigma_{13} & 0 & 0 & 0 \\
-\sigma_{21} & \lambda + \sigma_{22} - \Delta_1 & f_{23}x_2 & 0 & 0 & f_{26}x_2 \\
0 & -\sigma_{32} & \lambda + \sigma_{33} & 0 & 0 & 0 \\
0 & 0 & 0 & \lambda + \sigma_{44} & -\sigma_{45} & -\sigma_{46} \\
0 & 0 & f_{53}x_5 & -\sigma_{54} & \lambda + \sigma_{55} - \Delta_2 & f_{56}x_5 \\
0 & 0 & 0 & 0 & -\sigma_{65} & \lambda + \sigma_{66}
\end{vmatrix} \quad (14)
$$

By expanding according to the first three columns we obtain for the constant term

$$
\begin{aligned}
P(0) &= \begin{vmatrix}
\sigma_{11} & -\sigma_{12} & -\sigma_{13} \\
-\sigma_{21} & \sigma_{22} - \Delta_1 & f_{23}x_2 \\
0 & -\sigma_{32} & \sigma_{33}
\end{vmatrix}
\begin{vmatrix}
\sigma_{44} & -\sigma_{45} & -\sigma_{46} \\
-\sigma_{54} & \sigma_{55} - \Delta_2 & f_{56}x_5 \\
0 & -\sigma_{65} & \sigma_{66}
\end{vmatrix} - \\
&\quad - \begin{vmatrix}
\sigma_{11} & -\sigma_{12} & 0 \\
-\sigma_{21} & \sigma_{22} - \Delta_1 & f_{26}x_2 \\
0 & -\sigma_{32} & 0
\end{vmatrix}
\begin{vmatrix}
0 & \sigma_{44} & -\sigma_{45} \\
f_{53}x_5 & -\sigma_{54} & \sigma_{55} - \Delta_2 \\
0 & 0 & -\sigma_{65}
\end{vmatrix},
\end{aligned}
$$

and simple calculations lead to

$$
P(0) = \sigma_{11}\sigma_{44}\sigma_{32}\sigma_{65}x_2x_6\Delta_f.
$$

$P(0) > 0$ for the asymptotic stability. If $P(0) > 0$ is valid, then $\Delta_f > 0$ must hold as well and, hence, $\Delta_{x_3} > 0$, $\Delta_{x_6} > 0$. Due to $\Delta_1 < 0$ and $\Delta_2 < 0$ we obtain immediately the following necessary conditions for the existence of an inner stationary point

$$
f_{23} > |\frac{\Delta_1}{\Delta_2}|f_{53}, \quad f_{56} > |\frac{\Delta_2}{\Delta_1}|f_{26}. \quad (15)
$$

These inequalities mean again that the inward-directed (cannibalistic) predatory intensity is great enough compared with the outward-directed one.

If these conditions are valid, then $\Delta_f > 0$. The inner stationary point exists if $\Delta_1 < 0$ and $\Delta_2 < 0$ hold. It is obvious that all the coefficients of the characteristic polynomial are positive here.

Now suppose additionally that f_{23} and f_{56} (the cannibalistic intensities) are much higer than f_{53} and f_{26}. Under this condition we can show that the stationary point is asymptotically stable. In fact, (13) implies that

$$\Delta_f \simeq f_{23}f_{56}, \ \Delta_{x_3} \simeq -\Delta_1 f_{56}, \ \Delta_{x_6} \simeq -\Delta_2 f_{23}, \ x_3 \simeq -\frac{\Delta_1}{f_{23}}, \ x_6 \simeq -\frac{\Delta_2}{f_{56}},$$

$$f_{26}x_2 = f_{26}\frac{\sigma_{33}}{\sigma_{32}}x_3 = -\Delta_1\frac{\sigma_{33}f_{26}}{\sigma_{32}f_{23}} \simeq 0, \ f_{53}x_5 = f_{53}\frac{\sigma_{66}}{\sigma_{65}}x_6 = -\Delta_2\frac{\sigma_{66}f_{53}}{\sigma_{65}f_{56}} \simeq 0.$$

Thus, we obtain $P(\lambda) \simeq P_1(\lambda)P_2(\lambda)$,

$$
\begin{aligned}
P_1(\lambda) &= \begin{vmatrix} \lambda + \sigma_{11} & -\sigma_{12} & -\sigma_{13} \\ -\sigma_{21} & \lambda + \sigma_{22} - \Delta_1 & f_{23}x_2 \\ 0 & -\sigma_{32} & \lambda + \sigma_{33} \end{vmatrix}, \\
P_2(\lambda) &= \begin{vmatrix} \lambda + \sigma_{44} & -\sigma_{45} & -\sigma_{46} \\ -\sigma_{54} & \lambda + \sigma_{55} - \Delta_2 & f_{56}x_5 \\ 0 & -\sigma_{65} & \lambda + \sigma_{66}. \end{vmatrix}.
\end{aligned}
\tag{16}
$$

The coefficients of $\quad P_1(\lambda) = \lambda^3 + a_1\lambda^2 + a-2\lambda + a_3 \quad$ equal

$$
\begin{aligned}
a_1 &= \sigma_{11} + \sigma_{33} + \frac{\sigma_{13}\sigma_{21}\sigma_{32}}{\sigma_{11}\sigma_{33}}, \\
a_2 &= \sigma_{11}\sigma_{33} + \sigma_{32}f_{23}x_2 + \frac{\sigma_{33}^2\sigma_{12}\sigma_{21} + \sigma_{11}\sigma_{13}\sigma_{21}\sigma_{32} + \sigma_{33}\sigma_{13}\sigma_{12}\sigma_{21}}{\sigma_{11}\sigma_{33}}, \\
a_3 &= \sigma_{32}\sigma_{11}f_{23}x_2.
\end{aligned}
$$

It is obvious that $a_1 > 0, a_3 > 0$ and $a_1a_2 - a_3 > 0$ hold. Hence, by Routh-Hurwitz criterion the real parts of the roots of $P_1(\lambda)$ are negative. For $P_2(\lambda)$ everything is analogous. Therefore, the inner stationary point is stable at high inward-directed predatory intensities.

2.5 Inner and boundary stationary points

Beside the inner stationary points, some stationary points can also occur at the boundary of the state space. These states correspond to the case when at least one population dies out. We want to investigate the stability of these points in context of the stability of inner points.

Proposition 1. *If several inner stationary points exist, then there are no*

asymptotically stable ones.

Proof. Indeed, the origin is unstable for each single population, because the corresponding determinants $\Delta_1, \cdots, \Delta_m$ are all negative. From this it follows that, for example, the first population does not vanish if all the others are small enough. It means that the origin is unstable for the whole system. The other stationary points constitute a non-empty connected set and hence they are not asymptotically stable (see Fig.1).

Proposition 2. *If one inner asymptotically stable point exists, then the boundary points without one population are unstable .*

Proof. Without restriction of generality we can suppose that the first population is absent, i.e.

$$y_1 = 0, y_2 \neq 0, \cdots, y_m \neq 0,$$

and $y_2, \cdots, y_m$ are given by the system

$$c_{22}y_2 + \cdots + c_{2m}y_m = -\Delta_2$$
$$\vdots \tag{17}$$
$$c_{m2}y_2 + \cdots + c_{mm}y_m = -\Delta_m.$$

Analogously to the preceding, let

$$\delta = \begin{vmatrix} c_{22} & \cdots & c_{2m} \\ & \vdots & \\ c_{m2} & \cdots & c_{mm} \end{vmatrix}, \quad \delta_{y_i} = \begin{vmatrix} c_{2m} & \cdots & -\Delta_2 & \cdots & c_{1m} \\ & & \vdots & & \\ c_{m2} & \cdots & -\Delta_m & \cdots & c_{mm} \end{vmatrix}.$$

If (17) determines an inner asymptotically stable point, then the determinant δ of the system does not equal 0 and is positive according to the prorosition 1. Thus, the solution can be written as follows

$$y_i = \frac{\delta_{y_i}}{\delta}, \quad 2 \leq i \leq m. \tag{18}$$

Further we write $Q_X(\lambda)$ instead of $Q(\lambda)$ in order to emphasise that the polynomial $Q(\lambda)$ is calculated at the point X. From $y_1 = 0$ it follows that at the point $X = (0, \cdots, 0, x_{p_2}, \cdots, x_q)$ we have $d_{12} = 0, \cdots, d_{1m} = 0$ and

$$Q_X(\lambda) = Q_{1X}(\lambda)Q_{2X}(\lambda).$$

It is evident that

$$Q_{1X}(\lambda) = d_{11}(\lambda), \quad Q_{2X} = \begin{vmatrix} d_{22}(\lambda) & \cdots & d_{2m}(\lambda) \\ & \vdots & \\ d_{m2}(\lambda) & \cdots & d_{mm}(\lambda) \end{vmatrix}.$$

Due to $x_1 = 0, \cdots, x_{q_1} = 0$ we obtain

$$Q_{1X}(0) = \begin{vmatrix} \sigma_{11} + \sum_{k=p_2}^{q} f_{1k}x_k & -\sigma_{12} & \cdots & -\sigma_{1q_1} \\ -\sigma_{21} & \sigma_{22} & 0 & \cdots \\ \vdots & & \ddots & \\ 0 & \cdots & -\sigma_{q_1 q_1 - 1} & \sigma_{q_1 q_1} \end{vmatrix} = \nu_1 \{\Delta_1 + \sum_{k=p_2}^{q} f_{1k}x_k\}.$$

If x_k, $p_2 \le k \le q$, are represented by $y_2, \cdots, y_m$, by means of (9) we have

$$Q_{1X}(0) = \nu_1\{\Delta_1 + c_{12}y_2 + \cdots + c_{1m}y_m\}.$$

Therefore, (18) gives

$$\begin{aligned} Q_{1X}(0) &= \frac{\nu_1}{\delta}\{\Delta_1\delta + c_{12}\delta_{y_2} + \cdots + c_{1m}\delta_{y_m}\} \\ &= \frac{\nu_1}{\delta} \begin{vmatrix} \Delta_1 & c_{12} & \cdots & c_{1m} \\ \Delta_2 & c_{22} & \cdots & c_{2m} \\ & & \vdots & \\ \Delta_m & c_{m2} & \cdots & c_{mm} \end{vmatrix} = -\frac{\nu_1}{\delta}\Delta_{y_1} < 0, \end{aligned}$$

since Δ_{y_1} is positive. That means that the point X is unstable. The first population increases if the others remain in the state corresponding to the point X. Figure 2 shows the dynamic in this case. The marked points on the axes correspond to the unstable boundary points.

Remark. This property is also true for system (11) with two populations in which the middle age stages are attacked. Indeed, for example let $x_4 = x_5 = x_6 = 0$. For x_3 we obtain

$$f_{23}x_3 = -\Delta_1, \quad x_3 = -\frac{\Delta_1}{f_{23}}. \tag{19}$$

As we see from (14), the characteristic polynomial is equal to $P(\lambda) = P_1(\lambda)R(\lambda)$. $P_1(\lambda)$ is precisely determinant (16) and $R(\lambda)$ is given by

$$R(\lambda) = \begin{vmatrix} \lambda + \sigma_{44} & -\sigma_{45} & -\sigma_{46} \\ -\sigma_{54} & \lambda + \sigma_{55} + f_{53}x_3 & f_{56}x_5 \\ 0 & -\sigma_{65} & \lambda + \sigma_{66} \end{vmatrix}.$$

But for $R(\lambda) = \lambda^3 + b_1\lambda^2 + b_2\lambda + b_3$ it is

$$b_3 = R(0) = \sigma_{44}\sigma_{55}\sigma_{66} - \sigma_{45}\sigma_{54}\sigma_{66} - \sigma_{65}\sigma_{54}\sigma_{46} + \sigma_{44}\sigma_{66}f_{53}x_3.$$

Thus, (15,19) imply

$$b_3 = \sigma_{44}\sigma_{66}(\Delta_2 + f_{53}x_3) = \sigma_{44}\sigma_{66}(\Delta_2 - \frac{f_{53}}{f_{23}}\Delta_1) < 0$$

and the boundary stationary point with $x_4 = x_5 = x_6 = 0$ is unstable. For the other boundary stationary points everything is analogous.

For system (1) with two populations and two age stages each, in which only the youngest representatives are attacked by the oldest ones, this analysis can be completed as follows.

Proposition 3. *If the populations are cannibalistic and the only inner stationary point of system (1) is unstable, then there exist asymptotically stable boundary points.*
Proof. Let $f_{12} > 0$. Since only one inner stationary point exists, then $\Delta_1 < 0, \Delta_2 < 0$ and $\Delta \neq 0$ in (3). As we saw in the proof of proposition 1, the instability there is equivalent to $\Delta < 0$, $\Delta_{x_1} < 0$, $\Delta_{x_3} < 0$. In the stationary point $X = (x_1, x_2, 0, 0)$ with $x_3 = 0$ we have

$$x_1 = -\frac{\Delta_1}{c_{11}} = -\frac{\sigma_{22}\Delta_1}{f_{12}\sigma_{21}}, \quad x_2 = \frac{\sigma_{21}x_1}{\sigma_{22}} = -\frac{\Delta_1}{f_{12}}.$$

At X in (5) we have $d_{21}(\lambda) = 0$. The characteristic polynomial $P_X(\lambda)$ at the point X has the form $P_X(\lambda) = d_{11}(\lambda)R_2(\lambda)$. $d_{11}(\lambda)$ is polynomial (6) here. The real parts of its roots are negative. For

$$R_2(\lambda) = \begin{vmatrix} \sigma_{33} + f_{32}x_2 + \lambda & -\sigma_{34} + f_{34}x_3 \\ -\sigma_{43} & \sigma_{44} + \lambda \end{vmatrix} = \lambda^2 + b_1\lambda + b_2$$

we have $b_1 > 0$ and

$$b_2 = \sigma_{44}\{\Delta_2 + f_{32}x_2\} = \sigma_{44}\{\Delta_2 - \frac{f_{32}\Delta_1}{f_{12}}\} = -\frac{\sigma_{22}\sigma_{44}}{\sigma_{21}f_{12}}\Delta_{x_1} > 0. \qquad (20)$$

Then the real parts of the roots of $R_2(\lambda)$ are also negative and the point X is asymptotically stable. Analogously we find another asymptotically stable boundary point $(0, 0, x_3, x_4)$ if $f_{34} > 0$.

Figure 3 illustrates the dynamic in this case. This figure, however, may by misleading. The real state space is 4-dimensional and no simple conclusions about the global properties of the system should be made on the basis of this figure.
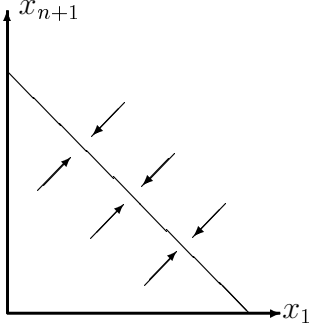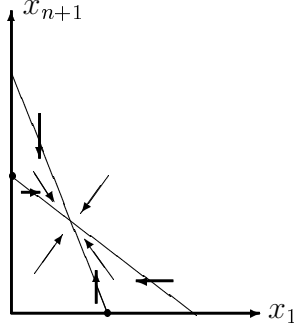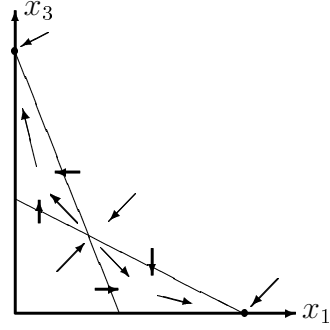
Fig. 1.

Fig. 2.

Fig. 3.

Proposition 4. *If the populations are cannibalistic and system (1) has no inner stationary points, then asymptotically stable boundary points exist.*
Proof. Let $\bar{x}_1 = -\Delta_1/c_{11}$ and $\tilde{x}_1 = -\Delta_2/c_{21}$. $\bar{x}_1$ and $\tilde{x}_1$ may also be negative. They determine the x-coordinate of the points in which the straight lines $c_{11}x_1 + c_{12}x_3 = 0$ and $c_{21}x_1 + c_{22}x_3 = 0$ intersect the x-axis (see Fig. 4a-4c). Suppose $\tilde{x}_1 \leq \bar{x}_1$. We will show the existence of asymptotically stable points without the second population. In the case $\bar{x}_1 \leq \tilde{x}_1$, there exist analogous stable points without the first population. Thus, there are only the following possibilities:
a) $\bar{x}_1 \leq 0$, $\tilde{x}_1 \leq 0$,   b) $\bar{x}_1 > 0$, $\tilde{x}_1 \leq 0$,   c) $\bar{x}_1 > 0$, $\tilde{x}_1 > 0$, $\tilde{x}_1 < \bar{x}_1$.

In case a) $\Delta_1 \geq 0$, $\Delta_2 \geq 0$ hold. The origin $\bar{0} = (0,0,0,0)$ is the only stationary point in the state space. It is even globally attractive, [1,18]. Indeed, positive q_1, q_2 and q_3, q_4 exist here, such that it holds

$$
\begin{aligned}
(q_1x_1 + q_2x_2)' &= c_1x_1 - q_1x_1(f_{12}x_2 + f_{14}x_4), \quad c_1 \leq 0, \\
(q_3x_3 + q_4x_4)' &= c_3x_3 - q_3x_3(f_{32}x_2 + f_{34}x_4), \quad c_3 \leq 0.
\end{aligned}
$$

Clearly, this yields $x_i \to 0$ for $1 \leq i \leq 4$ (see Fig. 4a).

In cases b) and c) it holds $\Delta_1 < 0$. For the stationary boundary point $X = (\bar{x}_1, \bar{x}_2, 0, 0)$ with $\bar{x}_2 = \sigma_{21}\bar{x}_1/\sigma_{22}$ we obtain $P_X(\lambda) = d_{11}(\lambda)R_2(\lambda)$ analogously to the proof of proposition 3. The real parts of the roots of $d_{11}(\lambda)$ and $R_2(\lambda)$ are negative. Therefore, X is asymptotically stable.

In case b) the point X is globally attractive, too. In order to prove it, we can show first due to $\Delta_2 \geq 0$ analogously to the case a) that x_3 and x_4 vanish, $(x_3, x_4) \to (0,0)$. That yields $f_{14}x_4 \to 0$ and from the first two equations of system (1) we can conclude $(x_1, x_2) \to (\bar{x}_1, \bar{x}_2)$. The origin is evidently unstable in these cases. Figures 4b and 4c illustrate the dynamic in these cases.

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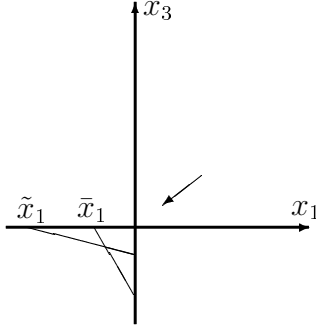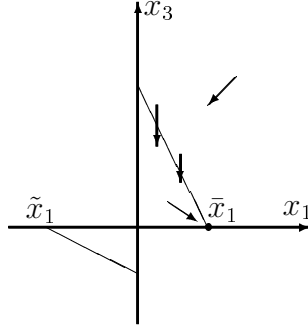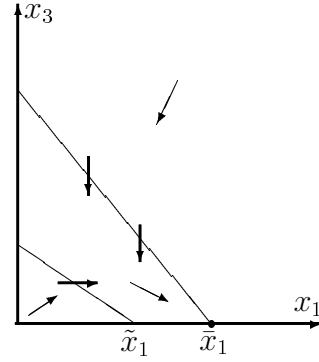| Fig. 4a. | Fig. 4b. | Fig. 4c. |

Properties 1-4 show that the dynamic of system (1) is considerably similar to the dynamic of the so-called Menten-Volterra-models with competition, [18].

3 Life boat mechanism

We now want to show that cannibalism can act as a *life boat mechanism* in our model. We also analyse how the change of cannibalistic pressure affects the system. We consider a system of a single population of two age stages. x_1 and x_2 are the densities of these stages, and the oldest stage is cannibalistic. The system of differential equations has the form

$$\begin{aligned} x_1' &= -\sigma_{11}x_1 + \sigma_{12}x_2 - f_{12}x_1x_2 \\ x_2' &= \sigma_{21}x_1 - \sigma_{22}x_2, \end{aligned} \tag{21}$$

where $\sigma_{11} = const, \quad \sigma_{21} = const, \quad \sigma_{12} = r_2\Phi_2, \quad \sigma_{22} = w_2\Phi_2 + m_2(1 - \Phi_2)$. Φ_2 is the fitness-function of the stage x_2,

$$\Phi_2 = \frac{\Theta_2}{h_2 + \Theta_2}, \quad 0 \le \Phi_2 \le 1.$$

Here Θ_2 is the total food supply. Thus, $\Theta_2 = e_2 + f_{12}\gamma_{12}x_1$, where $e_2 > 0$ is the external food suply, and $f_{12}\gamma_{12}x_1$ is the profit by cannibalism. Hence,

$$\Phi_2 = \frac{e_2 + f_{12}\gamma_{12}x_1}{h_2 + e_2 + f_{12}\gamma_{12}x_1}.$$

From (21) it follows at the stationary point

$$x_1 = \frac{\sigma_{22}}{\sigma_{21}}x_2.$$

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Hence, for the non-trivial solution we have

$$\sigma_{21}f_{12}x_1 + \sigma_{11}\sigma_{22} - \sigma_{12}\sigma_{21} = 0,$$

i.e. with $x_1 = z$

$$\sigma_{21}f_{12}z + \frac{\sigma_{11}[w_2(e_2 + f_{12}\gamma_{12}z) + m_2h_2]}{h_2 + e_2 + f_{12}\gamma_{12}z} - \frac{\sigma_{21}r_2(e_2 + f_{12}\gamma_{12}z)}{h_2 + e_2 + f_{12}\gamma_{12}z} = 0.$$

For z we come to the quadratic equation

$$\sigma_{21}f_{12}^2\gamma_{12}z^2 + zf_{12}[\sigma_{21}(h_2+e_2)+\sigma_{11}w_2\gamma_{12}-\sigma_{21}r_2\gamma_{12}]+[\sigma_{11}(w_2e_2+m_2h_2)-\sigma_{21}r_2e_2] = 0,$$

or shorter

$$\sigma_{21}f_{12}^2\gamma_{12}z^2 + f_{12}Az + B = 0, \tag{22}$$

where the parameters

$$A = \sigma_{21}(h_2 + e_2) + \sigma_{11}w_2\gamma_{12} - \sigma_{21}r_2\gamma_{12} \text{ and } B = \sigma_{11}(w_2e_2 + m_2h_2) - \sigma_{21}r_2e_2$$

are independent of f_{12}. Clearly,

$$B = (h_2 + e_2)\begin{vmatrix} \sigma_{11} & -\sigma_{12}(0) \\ -\sigma_{21} & \sigma_{22}(0) \end{vmatrix} = (h_2 + e_2)\Delta(0).$$

When $B > 0$ the trivial solution $\bar{0} = (0,0)$ is asymptotically stable, when $B < 0$ it is unstable. For the solutions of (22) we have

$$z_{1,2} = \frac{-A \pm \sqrt{A^2 - 4\sigma_{21}\gamma_{12}B}}{2\sigma_{21}f_{12}\gamma_{12}}.$$

We mention the most important possibilities for the positive solutions because only those are interesting.

1. $B = 0$, $A < 0$. In this case there is $z_1 = -A/\sigma_{21}f_{12}\gamma_{12} > 0$, $z_2 = 0$ and z_1 decreases if f_{12} increases. This case is critical and the question of stability of $\bar{0} = (0,0)$ cannot be answered by means of the linearized system. From (21) we obtain

$$(\sigma_{21}x_1 + \sigma_{11}x_2)' = (\sigma_{12}\sigma_{21} - \sigma_{11}\sigma_{22})x_2 - f_{12}\sigma_{21}x_1x_2.$$

Due to

$$\begin{aligned} \sigma_{12}\sigma_{21} - \sigma_{11}\sigma_{22} &= \frac{\sigma_{21}r_2(e_2 + f_{12}\gamma_{12}x_1) - \sigma_{11}[w_2(e_2 + f_{12}\gamma_{12}x_1) + m_2h_2]}{h_2 + e_2 + + f_{12}\gamma_{12}x_1} \\ &= \frac{\sigma_{21}r_2 - \sigma_{11}w_2}{h_2 + e_2 + f_{12}\gamma_{12}x_1}f_{12}\gamma_{12}x_1 \end{aligned}$$

22

and $A = \sigma_{21}(h_2 + e_2) + (\sigma_{11}w_2 - \sigma_{21}r_2)\gamma_{12} < 0$ we have $\sigma_{11}w_2 - \sigma_{21}r_2 < 0$. This means that the origin is unstable and in this case the vector field looks like Fig. 5.

2. When $B < 0$ the point $\bar{0} = (0,0)$ is unstable, $z_2 < 0$ and

$$z_1 = \frac{-A + \sqrt{A^2 - 4\sigma_{21}\gamma_{12}B}}{2\sigma_{21}f_{12}\gamma_{12}} > 0.$$

z_1 decreases if f_{12} increases. The vector field is similar to that described above, see Fig. 6.

3. When $B > 0$, $A < 0$ and $D = A^2 - 4\sigma_{21}\gamma_{12}B > 0$ the point $(0,0)$ is asymptotically stable and $z_1 > 0$, $z_2 > 0$, $z_1 > z_2$. The vector field is represented in Fig. 7. In this case the point X_1 with the coordinate $x_1 = z_1$ is asymptotically stable. The population can remain in this state by cannibalism. It would not survive these circumstances without cannibalism. That corresponds to *life boat mechanism*. The point X_2 with the first coordinate x_2 is unstable. For the nontrivial stable stationary point we have

$$x_1 = z_1 = \frac{-A + \sqrt{A^2 - 4\gamma_{12}\sigma_{21}B}}{\sigma_{21}f_{12}\gamma_{12}} = \frac{K_1}{f_{12}},$$

where K_1 is independent of f_{12}. Hence, we obtain

$$\Phi_2 = \Phi_2(x_1) = \frac{e_2 + f_{12}\gamma_{12}x_1}{h_2 + e_2 + f_{12}\gamma_{12}x_1} = \frac{e_2 + \gamma_{12}K_1}{h_2 + e_2 + \gamma_{12}K_1} = K_2$$

and $\Phi_2 = K_2$ does not depend on f_{12} either,

$$x_2 = \frac{\sigma_{21}}{\sigma_{22}}x_1 = \frac{\sigma_{21}K_1}{f_{12}[w_2K_2 + m_2(1 - K_2)]},$$

so that x_1 and x_2 converge to 0 for $f_{12} \to \infty$. It means that under greater cannibalistic pressure the population stabilises itself at a lower level, but it does not die out.

4. When $A < 0, B > 0, D = 0$ the inner stationary point is unstable, see Fig. 8.
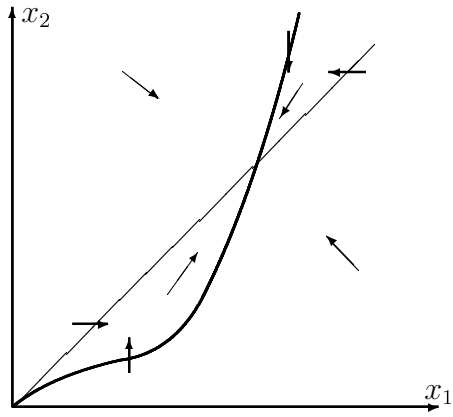
Fig. 5. Stable nontrivial solution, critical origin.
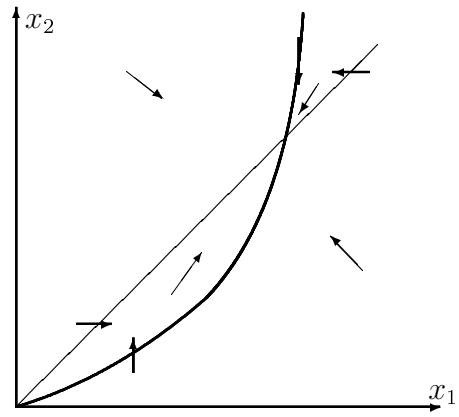

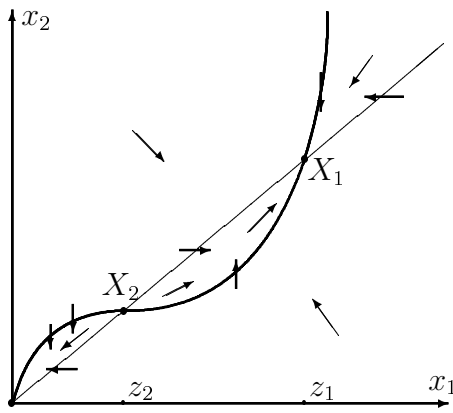Fig. 6. Stable nontrivial solution, unstable origin.

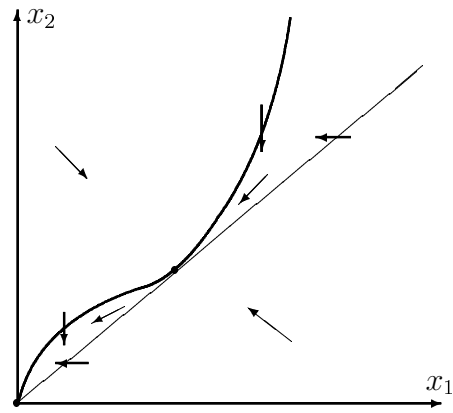Fig. 7. Stable nontrivial solution, stable origin.

Fig. 8. Unstable inner point, stable origin.

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4 Numeric examples and final remarks

For the analytic investigations in the preceding part we needed certain assumptions to simplify the system of differential equations. Now we want to represent a few results of numeric simulations that were carried out without such simplifications. The system describes the dynamic of two populations: *Neomysis integer* and *Praunus flexuosus*. The experiments for these species were carried out by G. Winkler (Research Institute Senckenberg, Germany). Further we use the data which were gained in these experiments.

Each population is subdivided into three age stages. x_1, x_2 and x_3 are the age stages of *Neomysis integer*, x_4, x_5, x_6 – of *Praunus flexuosus*, x_1 and x_4 are the youngest stages. Only the oldest stages x_3 and x_6 are capable of reproduction. The coefficients σ_{ij} are dependent here on fitness-functions Φ_j, $1 \leq j \leq 6$, [20]. The half-value constants $h_i, 1 \leq i \leq 6$, were set at different levels. We see that they did not change the qualitative results. Further they are equal to 0.1. The other parameters are:
$w_1 = 0.13412$, $w_2 = 0.0602$, $w_3 = 0.0154$, $w_4 = 0.1405$, $w_5 = 0.00766$, $w_6 = 0.0231$;
$m_1 = 0.0866, m_2 = 0.077, m_3 = 0.0693, m_4 = 0.099, m_5 = 0.077, m_6 = 0.693$;
$f_{15} = 0.294$, $f_{16} = 0.642$, $f_{26} = 0.266$; $r_{13} = 1.0476$, $r_{46} = 0.5333$;
$C_1 = 0.014$, $C_2 = 0.092$, $C_3 = 1.027$, $C_4 = 0.082$, $C_5 = 0.0703$, $C_6 = 3.345$.
Praunus flexuosus is thus predator on *Neomysis integer*. The cannibalistic attack rates f_{46} and f_{56} are varied.

The system of differential equations has the form

$$
\begin{aligned}
x_1' &= -\sigma_{11}x_1 + \sigma_{13}x_3 - x_1\{f_{15}x_5 + f_{16}x_6\} \\
x_2' &= \sigma_{21}x_1 - \sigma_{22}x_2 - x_2\{f_{26}x_6\} \\
x_3' &= \sigma_{32}x_2 - \sigma_{33}x_3 \\
x_4' &= -\sigma_{44}x_4 + \sigma_{46}x_6 - f_{46}x_4x_6 \\
x_5' &= \sigma_{54}x_4 - \sigma_{55}x_5 - f_{56}x_5x_6 \\
x_6' &= \sigma_{65}x_5 - \sigma_{66}x_6
\end{aligned}
$$

In following Fig. 9 the stationary states without cannibalism ($f_{46} = 0$, $f_{56} = 0$) are represented: on the left – for *Neomysis integer*, on the right – for *Praunus flexuosus*. The parameter e is the external food supply. This is the same for all the age stages. The parameter interval $[e_{min}, e_{max}]$, which lies under the marked points (here $e_{min} \approx 0.054$, $e_{max} \approx 0.183$), determines the survival-window for the whole system.
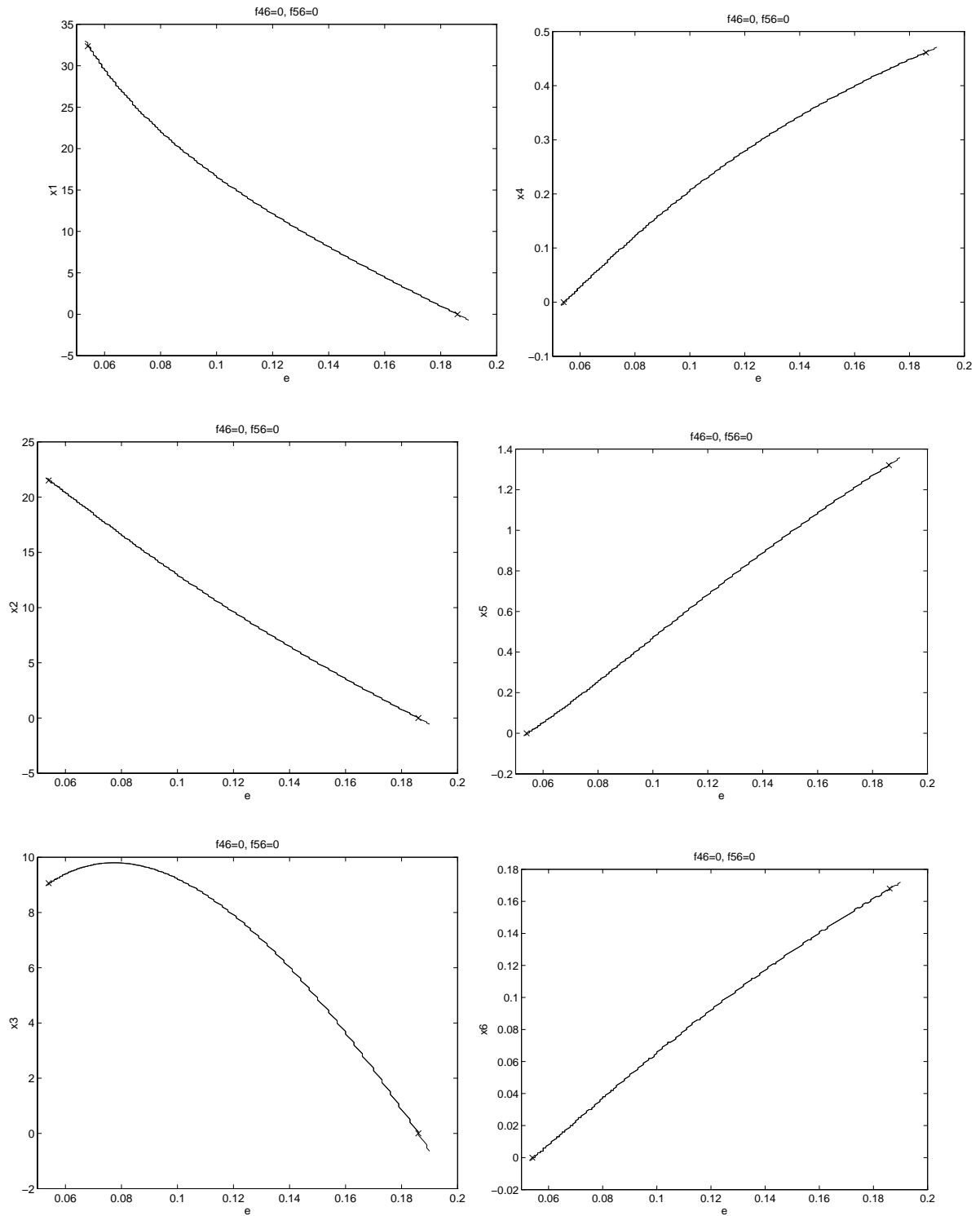
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Fig. 9 Stationary points. Case without cannibalism, e – external food supply.

The stationary points are asymptotically stable at $e_{min} \leq e \leq e_{max}$. At $e < e_{min}$ the both populations tend to extinction. At $e > e_{min}$ *Neomysis integer* would grow unlimitedly without the predatory *Praunus flexuosus*. The predator limit the prey and the former can live through the interval $[e_{min}, e_{max}]$ only thanks to the latter. When $e > e_{max}$ *Neomysis integer* dies out and *Praunus flexuosus* grows unlimitedly. But if later the external food supply becomes less, the predators disappear as well, because the prey is absent. If the predator is cannibalistic, it limits itself. The survival-window becomes larger, because then the upper boundary e_{max} increases. e_{min} and e_{max} are the same for all the stages, so any of the stages can be chosen to represent the results. In Fig. 10 we see the survival-window for the first age stage in cases $f_{46} = 0.5 f_{26}$ and $f_{46} = f_{26}$. In comparison with $e_{max} \approx 0.183$ in the case without cannibalism we have $e_{max} \approx 0.207$ and $e_{max} \approx 0.214$ respectively.
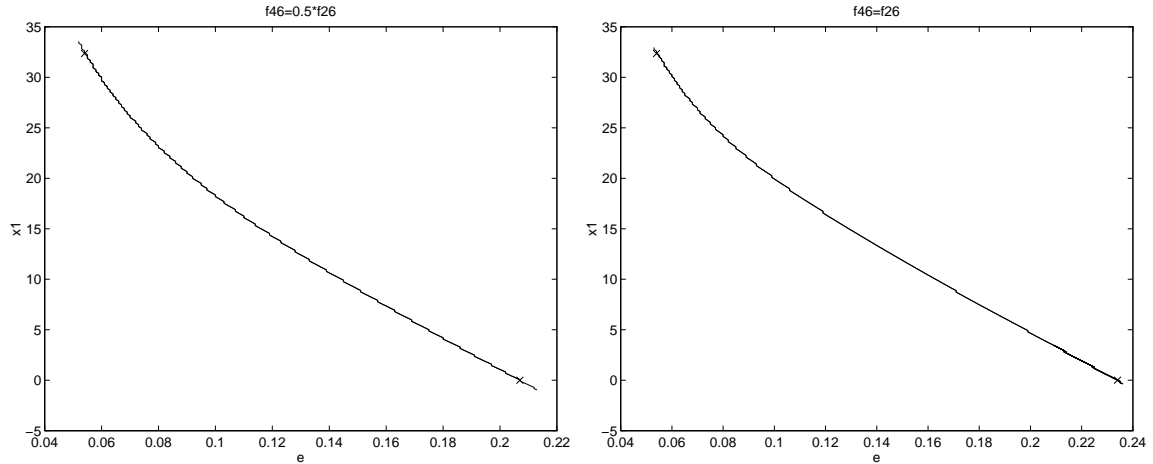

Fig. 10 The increase of the survival-window. $f_{46} = 0.5 f_{26}$ and $f_{46} = f_{26}$, e − external food supply.

If f_{56} increases, the result is analogous, see Fig. 11. When $f_{56} = 0.1 f_{26}$ and $f_{56} = 0.5 f_{26}$ we find $e_{max} \approx 0.2$ and $e_{max} \approx 0.435$ respectively. If the cannibalistic terms are great enough, the survival-window can become infinitely large. The predator does not eliminate its prey and the two populations stabilise themselves at a higher level when the external food supply is larger. In Fig. 12 we see the stationary states of the youngest age stages x_1 and x_4 in case $f_{56} = f_{26}$. The same is true of the other stages.
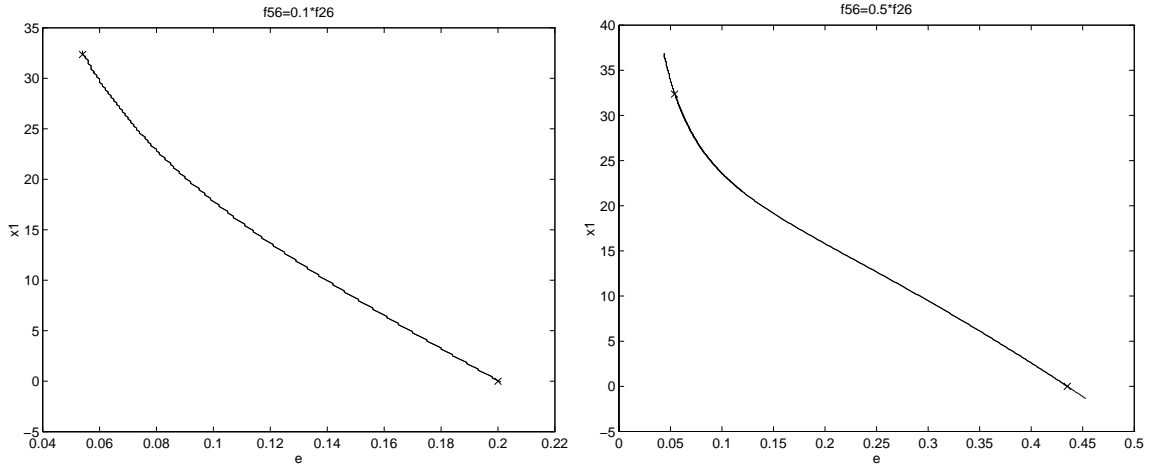
Fig. 11 The increase of the survival-window when $f_{56} = 0.1f_{26}$ and $f_{56} = 0.5f_{26}$. e – external food supply.
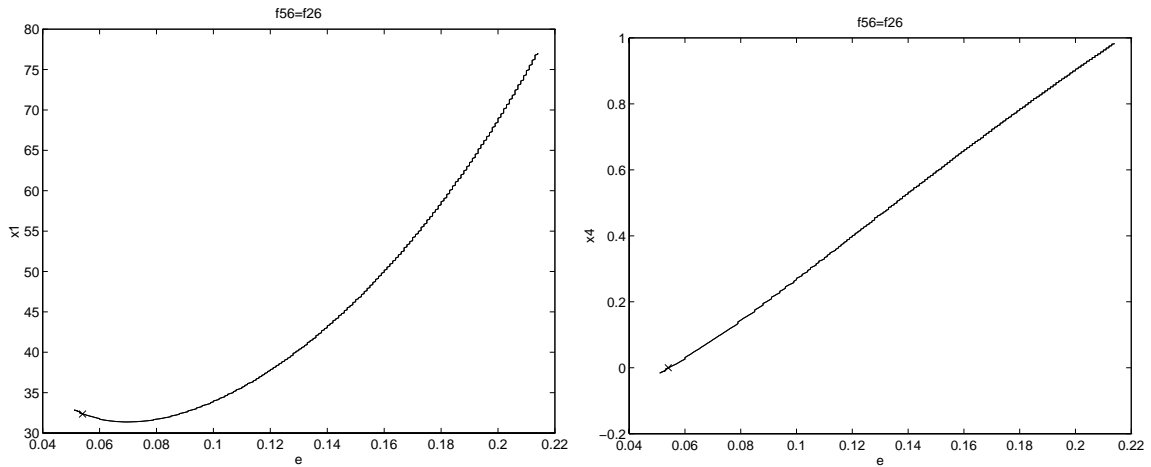

Fig. 12 The unbounded survival-window $(e_{max} = \infty)$ when $f_{46} = f_{26}$. e – external food supply.

The numeric simulations confirm the stabilising role of cannibalism for the dynamic of the system, so that in this sense cannibalism can be regarded as a positive factor for the entire system.

Fig. 13 shows the change of the dynamic for the first age stage x_1 of *Neomysis integer*. On the left-hand side f_{46} increases, on the right hand f_{56} varies. The external food supply equals $e = 0.12$ in all cases. The deviations from the stationary points are equal at the beginning as well. We see that the system stabilises itself faster under the stronger cannibalistic pressure. For the other age stages the results are analogous.
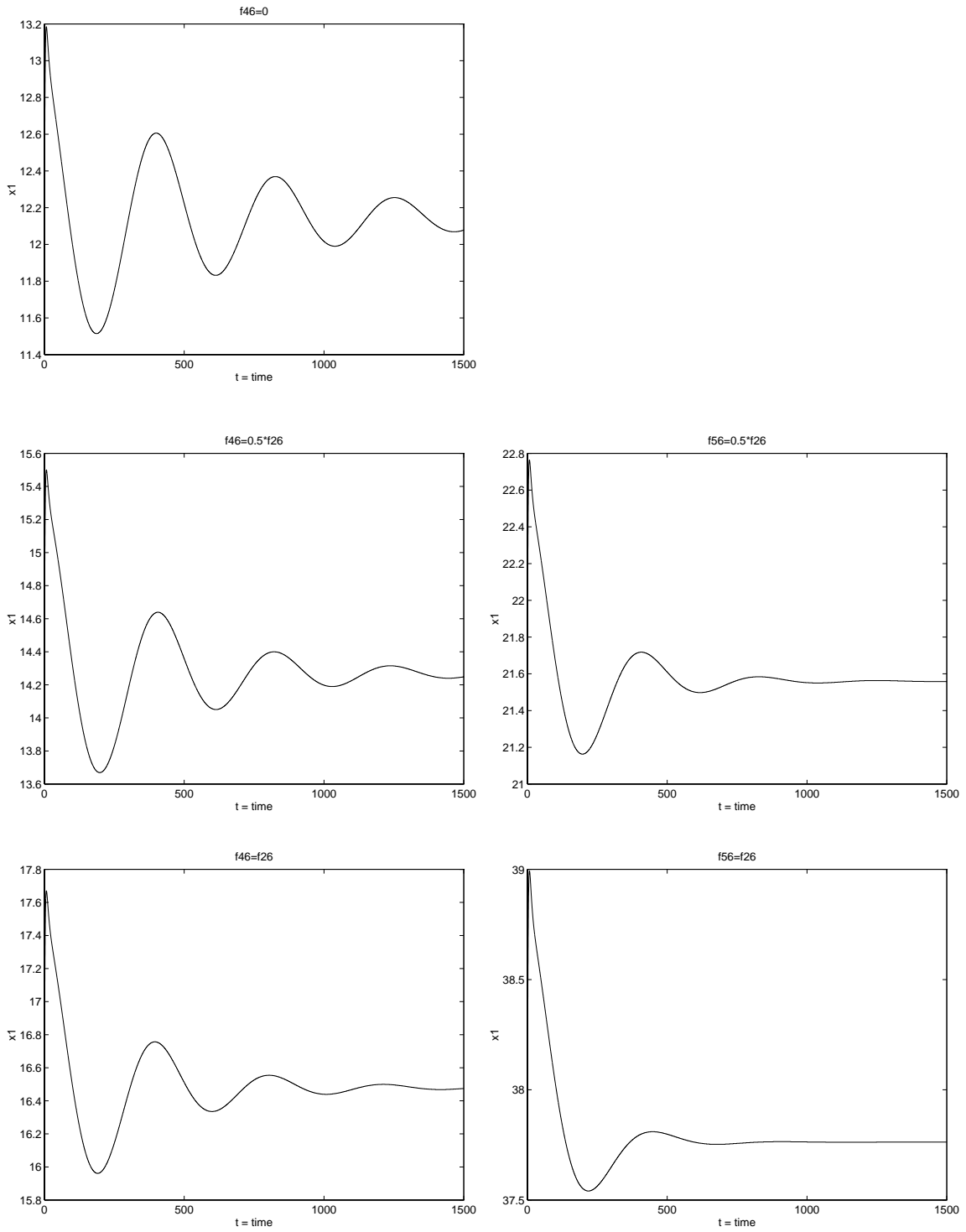
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Fig. 13 The dynamic of the age stage x_1 under different cannibalistic pressure.

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