

Universität Hamburg
Fachbereich Mathematik



Hamburger Beiträge
zur Modellierung und Simulation

Heft 4 Juli 1998

QUALITATIVE PROPERTIES OF A NICHE MODELL

Johannes Mainik / Claus Peter Ortlieb

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 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.

Zentrum für Modellierung und Simulation
Fachbereich Mathematik der Universität Hamburg
Bundesstraße 55

D - 20146 Hamburg

Telefon 040 4123 5108
Fax 040 4123 5117
e-mail zms@math.uni-hamburg.de

Qualitative properties of a niche-model

J. Mainik, C. P. Ortlieb

Department of Mathematics, University of Hamburg, Bundesstrasse 55,
20146 Hamburg, Germany. E-mail: Mainik: mainik@math.uni-hamburg.de
Ortlieb: ortlieb@math.uni-hamburg.de

Zusammenfassung

Within the framework of the analysis of ecological systems W. Greve developed a model of marine populations. This model is expected to allow a wider embracement of the ecological niches' potential and, therefore, also of the whole system's one. This niche-model employs age stages structures and complex relations of populations. We analyse qualitative features of this model which is described by a system of differential equations. The main themes of this paper are either the conditions of extinction, boundedness, permanence or the conditions of existence and uniqueness of stationary points. This analysis gives both a notion of the model's conduct and a mathematical appreciation of this complex model. The appreciation of the system can be valued as positive and encouraging.

Keywords: niche-model, system ecology, marine populations, permanence, stability analysis

1 Introduction

In the first mathematical population models by Maltus (1798), Lotka (1925) and Volterra (1926) populations were regarded as homogeneous, and so they could be described by a single variable quantity (e. g. population's size, density etc.). The populations' unrealistic, unbounded exponential growth was restricted by a logistic term which was originally analysed by Verhulst (1845), see [17]. This term represents in an implicit way the effects of intraspecific interactions. Here the population's internal dynamic is a kind of black-box. For an exacter understanding of these interactions, physiological backgrounds and their influence on the dynamic, the models must include population structures.

Population structures can be built on different bases (age, size, discrete, continuous, ...), and the kinds of internal relations of different stages can be many and various for different populations. Mathematical approaches (systems of differential or difference equations, partial differential equations, delay differential equations, ...) differ very much, too. All these circumstances require the wide spectrum and the great number of papers that belong to the theme of modelling structured populations, [5,9,15,19,20,22].

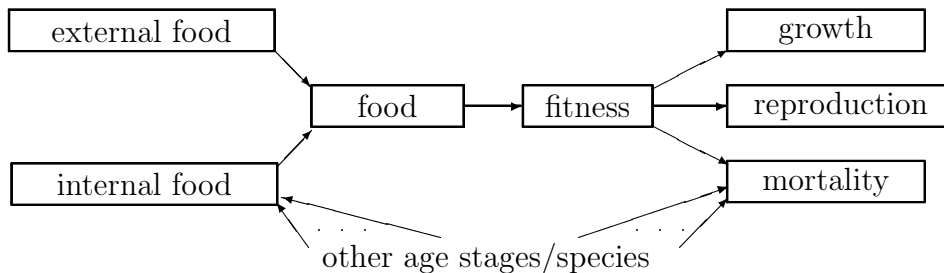
Within the analysis of ecological systems W. Greve designed a niche-model of marine populations, [12-14], based on the following ideas:

1. The hierarchical structure of the food chain is replaced by a food web. Since the trophical relations between marine populations are not unilateral, the development stages and their interactions must be included in the analysis of population dynamic. Complicated trophical relations are typical of many populations, and they cannot be treated as exceptions. Interesting results about *Calanus helgolandicus* and *Pleurobrachia pileus* which both play a very important role in the North Sea can be found, for example, in [14].

2. Stage-specific parameters (rates of reproduction, growth and mortality) are functions of metabolism rates on these stages, so that the food supply regulates the dynamic of the stages, being a regulating element of the whole system. The metabolism rates are described for all stages in a uniform way by Michaelis-Menten-terms.

3. Trophical relations and other parameters of the system have physiological reasons, and they can be registered empirically.

A survey of the interdependences in the model can be given by the following diagram.



This model should allow to cover the functional potential of a single ecological niche as well as that of the whole system. At present, necessary data are being collected in extensive experiments (W. Greve et al., Research Insti-

tute Senckenberg, Germany), and an extension of the model is being worked on.

Further we describe the model in the form of differential equations and analyse some of the model's qualitative properties. Generally we analyse conditions of extinction, boundedness, permanence and stable states. Since we are dealing with a complicated system of nonlinear differential equations, considerable restrictions must be assumed for various kinds of questions.

Nevertheless, this analysis with exact methods provides an insight into the model's conduct in a quality which cannot be reached just by simulations. Furthermore, these results must be regarded as a mathematical assessment that is necessary for such a complicated system. This model has already been analysed by C. Bente [2], but there have been other mainpoints.

The niche-model by W. Greve was designed to analyse the dynamic of marine populations. Nevertheless, it includes structures of age stages and complex trophical relations which are important not only in this case, e. g. [22]. Thus, this model can also be of interest in the investigation of other ecosystems.

The following results show among other things cannibalism's extraordinary role in the self-restriction and stabilization of a single population. Cannibalism is really a very wide-spread phenomenon among marine populations which are the main object of our analysis. But also for many other populations cannibalism is a very important factor which is worth analysing, see [3,4,6-8,10,11,16,18,21]. At present there are interesting results on the stabilizing role of cannibalism in systems with several populations. As this theme can be regarded as a considerably independent one, these results will be prepared for a further paper.

2 The model, Leslie-matrices

Let's denote the densities of different age stages of all populations regarded in the model by x_1, \dots, x_m and number the stages of every population in a way corresponding to the ages. For every age stage x_j a metabolism rate Φ_j is defined which we will further call fitness-function,

$$\Phi_j = \frac{\Theta_j}{h_j + \Theta_j}.$$

Here h_j is a half-value constant and Θ_j is the whole food supply for a particular individual of the stage x_j . The fitness-function satisfies $0 < \Phi_j < 1$ and the rates of growth, reproduction and mortality have the form

$$w_j \Phi_j, \quad r_j \Phi_j, \quad m_j(1 - \Phi_j),$$

where w_j , r_j and m_j are the constant growth, reproduction and mortality rates on this stage. Thus, an increase of Φ_j corresponds to a better condition of x_j .

We describe the mathematical model as a system of differential equations

$$\begin{aligned}x'_1 &= g_1(x_1, \dots, x_m) \\ &\vdots \\x'_m &= g_m(x_1, \dots, x_m).\end{aligned}$$

Due to the functional differences between the youngest stage and the other ones, different equation forms are achieved. Let x_k, \dots, x_l be all the age stages of the population. Then we have for the youngest stage

$$x'_k = -\sigma_{kk}x_k + \sigma_{kk+1}x_{k+1} + \dots + \sigma_{kl}x_l - \sum_j f_{kj}x_kx_j$$

and for the other ones

$$x'_i = \sigma_{ii-1}x_{i-1} - \sigma_{ii}x_i - \sum_j f_{ij}x_ix_j, \quad k+1 \leq i \leq l.$$

The coefficients in the equations have the following meaning:

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

$$\sigma_{ii} = w_i\Phi_i + m_i(1 - \Phi_i), \quad k \leq i \leq l.$$

The growth rate of the eldest stage x_l must be understood as the rate of death through old age.

$\sigma_{kk+1}, \dots, \sigma_{kl}$ determine the reproduction of the youngest stage x_k by the stages x_{k+1}, \dots, x_l and are given by

$$\sigma_{kj} = r_j\Phi_j, \quad k+1 \leq j \leq l.$$

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

$$\sigma_{ii-1} = w_{i-1}\Phi_{i-1}, \quad k+1 \leq i \leq l.$$

f_{ij} are constant and determine the intensity of x_j 's attacking x_i . In [12,13] they are called negative ARE-value.

The total food supply Θ_j for a single individual of the stage x_j is given by

$$\Theta_j = e_j + \sum_i p_{ij}x_i.$$

$e_j > 0$ is the external food supply, the term $p_{ij}x_i$ determines the food supply of stage x_i . The coefficients

$$p_{ij} = f_{ij}\gamma_{ij}, \quad \gamma_{ij} = \frac{C_i}{C_j},$$

where C_i and C_j are the carbon contents of individuals from x_i and x_j , are called positive ARE-values in [12,13].

If the first population has n age stages, the following matrix corresponds to it

$$\begin{pmatrix} -\sigma_{11} & \sigma_{12} & \sigma_{13} & \cdots & \sigma_{1n} \\ \sigma_{21} & -\sigma_{22} & 0 & \cdots & 0 \\ 0 & \sigma_{32} & -\sigma_{33} & \cdots & 0 \\ \vdots & & \ddots & \ddots & \\ 0 & \cdots & 0 & \sigma_{nn-1} & -\sigma_{nn} \end{pmatrix}.$$

The elements of the matrix satisfy

$$\sigma_{ii} > 0, 1 \leq i \leq n, \quad \sigma_{ii-1} > 0, 2 \leq i \leq n, \quad \sigma_{1j} \geq 0, 1 < j \leq n,$$

all other elements equal 0. Matrices of this kind are called Leslie-matrices. By analogy, Leslie-matrices for the other populations are to be defined. If x_{n+1}, \dots, x_{n+m} are, for example, the age stages of the second population, it is corresponded by a $(m \times m)$ -matrix

$$\begin{pmatrix} -\sigma_{n+1n+1} & \sigma_{n+1n+2} & \sigma_{n+1n+3} & \cdots & \sigma_{n+1n+m} \\ \sigma_{n+2n+1} & -\sigma_{n+2n+2} & 0 & \cdots & 0 \\ 0 & \sigma_{n+3n+2} & -\sigma_{n+3n+3} & \cdots & 0 \\ \vdots & & & \ddots & \\ 0 & \cdots & 0 & \sigma_{n+mn+m-1} & -\sigma_{n+mn+m} \end{pmatrix}.$$

Further we will use the following properties of Leslie-matrices which can be easily proved.

1. By expanding the determinant $\det(-A)$ according to the first row we obtain immediately for any $(n \times n)$ -Leslie-matrix

$$A = \begin{pmatrix} -a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & -a_{22} & \cdots & 0 \\ 0 & \ddots & \ddots & \\ \cdots & 0 & a_{nn-1} & -a_{nn} \end{pmatrix}$$

$$\begin{aligned} \det(-A) &= \prod_{i=1}^n a_{ii} - \sum_{j=2}^n a_{1j} \prod_{k=2}^j a_{kk-1} \prod_{k=j+1}^n a_{kk} \\ &= a_{11}a_{22} \cdots a_{nn} - a_{12}a_{21}a_{33} \cdots a_{nn} - \cdots - a_{1n}a_{21}a_{32} \cdots a_{nn-1}. \end{aligned}$$

2. If A_k , $1 \leq k \leq n$, are the leading principal submatrices on the first k rows and columns, then

$$\det(-A_{k+1}) = a_{k+1,k+1}\det(-A_k) - a_{1k+1}a_{21}a_{32}\cdots a_{k+1k}.$$

From this, it follows that all $\det(-A_j)$ for $k+1 \leq j \leq n$ are negative if $\det(-A_k)$ is negative.

Here we are going to prove two lemmas which are necessary later. A_k is still the leading principal submatrix of A with k first rows and columns, and $m(A) = \max\{j : a_{1j} \neq 0\}$ is the number of the eldest stage which is capable of reproduction. For a Leslie-matrix $\det(-A) < 0$, let us denote $s(A) = \min\{k : \det(-A_k) < 0\}$. In order to emphasize that we assume independence of a Leslie-matrix on parameters let us call it a constant one.

Lemma 1. *For a constant Leslie-matrix A with $m = m(A)$ the following properties hold*

1. *Suppose $\det(-A) > 0$, then positive numbers $q_1 > 0, \dots, q_n > 0$ exist such that $(q_1 \cdots q_n)A = (a_1 \cdots a_n)$, and $a_1 < 0, \dots, a_n < 0$.*

2. *Suppose $\det(-A) < 0$, then positive numbers $q_1 > 0, \dots, q_s > 0$ exist such that $(q_1 \cdots q_s 0 \cdots 0)A = (a_1 \cdots a_n)$, and $a_1 > 0, \dots, a_s > 0, a_{s+1} \geq 0, \dots, a_n \geq 0$.*

Proof. Further let $q_1 = 1$ and let z_1, \dots, z_n be the rows of A ,

$$A = \begin{pmatrix} z_1 \\ z_2 \\ z_3 \\ \vdots \\ z_n \end{pmatrix} = \begin{pmatrix} -a_{11} & a_{12} & a_{13} & \cdots & a_{1n} \\ a_{21} & -a_{22} & 0 & \cdots & 0 \\ 0 & a_{32} & -a_{33} & 0 & \cdots \\ & & \ddots & \ddots & \\ 0 & \cdots & 0 & a_{nn-1} & -a_{nn} \end{pmatrix}.$$

It is clear that $(q_1 \cdots q_n)A = q_1 z_1 + \cdots + q_n z_n$.

We start with the first case. First we eliminate in turn a_{1m}, \dots, a_{12} by means of the Gauss method. Here we add rows $p_m z_m, \dots, p_2 z_2$ to the row z_1 and show that p_m, \dots, p_2 are positive.

Let $b_m = a_{1m}$, so that

$$z_1 = (a_{11} \cdots a_{1m-1} b_m 0 \cdots 0), \quad b_m > 0.$$

Then

$$p_m = \frac{b_m}{a_{mm}} > 0, \quad z_1 + p_m z_m = (a_{11} \cdots a_{1m-2} b_{m-1} 0 \cdots 0),$$

and $b_{m-1} = a_{1m-1} + p_m a_{mm-1} > 0$ is positive, too. Therefore, $p_{m-1} = b_{m-1}/a_{m-1m-1} > 0$, and it can be continued in an analogous way. Thus, we obtain $p_m > 0, \dots, p_2 > 0$, so that

$$z_1 + p_2 z_2 + \dots + p_m z_m = (b_1 0 \dots 0)$$

and the matrix with the rows $z_1 + p_2 z_2 + \dots + p_m z_m, z_2, \dots, z_n$ is a triangle matrix.

These operations with the rows of the matrix A do not change its determinant, and obviously $\det(-A) = -b_1 a_{22} \dots a_{nn} > 0$, which yields $b_1 < 0$.

In the same manner we find by means of the matrix

$$B = \begin{pmatrix} 0 & 1 & 1 & \dots & 1 \\ a_{21} & -a_{22} & 0 & \dots & 0 \\ 0 & a_{32} & -a_{33} & 0 & \dots \\ & & \ddots & \ddots & \\ 0 & \dots & 0 & a_{nn-1} & -a_{nn} \end{pmatrix}$$

positive $r_2 > 0, \dots, r_n > 0$, such that $(01 \dots 1) + r_2 z_2 + \dots + r_n z_n = (c_1 0 \dots 0)$, and since $\det(-B) < 0$, $c_1 > 0$.

Let $q_i = p_i + \epsilon r_i$, $2 \leq i \leq n$, with $\epsilon > 0$. In this case all q_i are positive, and

$$\begin{aligned} q_1 z_1 + \dots + q_n z_n &= z_1 + p_2 z_2 + \dots + p_n z_n + r_2 z_2 + \dots + r_n z_n = \\ &= (b_1 0 \dots 0) + \epsilon(c_1 - 1 \dots - 1) = ((b_1 + \epsilon c_1) - \epsilon \dots - \epsilon) = (a_1 \dots, a_n). \end{aligned}$$

Thus, $a_i = -\epsilon$ are negative for $2 \leq i \leq n$. With a sufficiently small $\epsilon > 0$ a_1 is negative, since $b_1 < 0$, $a_1 = b_1 + \epsilon c_1 < 0$. The first part of the statement is proved.

Now let $\det(-A) < 0$. First we remark that $a_{1s} > 0$ is satisfied. In fact, $a_{1s} = 0$ implies $\det(-A_s) = a_{ss} \det(-A_{s-1})$, and so $\det(-A_{s-1}) < 0$, which contradicts the definition of $s = s(A)$.

Let $\tilde{z}_1, \dots, \tilde{z}_s$ be the rows of A_s . Now we look at the matrix A_s and determine by means of A_s positive $p_s > 0, \dots, p_2 > 0$, so that

$$\tilde{z}_1 + p_2 \tilde{z}_2 + \dots + p_m \tilde{z}_m = (b_1 0 \dots 0).$$

Since $\det(-A_s) = -b_1 a_{22} \dots a_{ss} < 0$ $b_1 > 0$ holds here. After that we find by means of the matrix

$$B_s = \begin{pmatrix} 0 & 1 & \dots & 1 \\ a_{21} & -a_{22} & 0 \dots & 0 \\ & \ddots & \ddots & \\ 0 \dots & 0 & a_{ss-1} & -a_{ss} \end{pmatrix}$$

positive $r_s > 0, \dots, r_2 > 0$, such that

$$(01 \cdots 1) + r_2 \tilde{z}_2 + \cdots + r_s \tilde{z}_s = (c_1 0 \cdots 0) \text{ with } c_1 > 0.$$

For small $\epsilon > 0$ all $q_i = p_i - \epsilon r_i$, $2 \leq i \leq s$ are positive and

$$\begin{aligned} (a_1, \dots, a_s) &= \tilde{z}_1 + (p_2 - \epsilon r_2) \tilde{z}_2 + \cdots + (p_m - \epsilon r_k) \tilde{z}_m = \\ (b_1 \ 0 \cdots 0) &- \epsilon (c_1 \ -1 \cdots -1) = (b_1 - \epsilon c_1 \ \epsilon \cdots \epsilon). \end{aligned}$$

Thus, as well $a_i = \epsilon$ for $2 \leq i \leq s$ are positive as $a_1 = b_1 - \epsilon c_1$ is for sufficiently small $\epsilon > 0$ due to $b_1 > 0$. It is clear that in this case

$$q_1 z_1 + \cdots + q_s z_s = (a_1 \cdots a_s a_{1s+1} \cdots a_{1n}),$$

and the second part of the statement holds. ■

Lemma 2. *Let A be a constant Leslie-matrix, $m = m(A)$, $k \leq m$ and $\det(-A_{k-1}) > 0$. In this case positive q_1, \dots, q_m do exist, such that*

$$(q_1 \cdots q_m 0 \cdots 0)A = (0 \cdots 0 c_k 0 \cdots 0)$$

with $c_k = 0$ when $\det(-A) = 0$, and $c_k > 0$ when $\det(-A) < 0$.

Proof. The proof of this lemma is analogous to that of lemma 1. First we eliminate in turn a_{1m}, \dots, a_{1k+1} . So we find positive $p_m > 0, \dots, p_{k+1} > 0$, such that

$$\bar{z}_1 = z_1 + p_{k+1} z_{k+1} + \cdots + p_m z_m = (a_{11} \cdots a_{1k-1} b_k 0 \cdots 0).$$

Then we eliminate in the following turn a_{11}, \dots, a_{1k-1} . For this aim we add the rows $p_2 z_2, \dots, p_k z_k$ to the row \bar{z}_1 . The coefficients p_2, \dots, p_k are all positive. Indeed, let $b_1 = -a_{11}$. We can write \bar{z}_1 in the form

$$\bar{z}_1 = (b_1 a_{12} \cdots a_{1k-1} b_k 0 \cdots 0) \quad \text{with } b_1 < 0.$$

After the first step with $p_2 = -b_1/a_{21} > 0$ we obtain

$$\bar{z}_1 + p_2 z_2 = (0 \ b_2 \ a_{13} \cdots a_{1k-1} b_k 0 \cdots 0).$$

In case $k > 2$ the operations with the rows have not changed the determinant of the matrix A_2 , and so $\det(-A_2) = -b_2 a_{21} > 0$. Thus, $b_2 < 0$, and we can continue by $p_3 = -b_2/a_{32} > 0$. In an analogous way we obtain for any $i < k$ $\det(-A_i) = -b_i a_{21} \cdots a_{ii-1} > 0$ and therefore $b_i < 0$, $p_{i+1} = -b_i/a_{i+1i} > 0$.

All these operations with rows do not change $\det(-A)$, and

$$\det(-A) = -c_k a_{21} \cdots a_{kk-1} a_{k+1k+1} \cdots a_{nn}.$$

So, from $\det(-A) = 0$ follows $c_k = 0$ and $\det(-A) < 0$ implies $c_k > 0$. ■

3 Simple development modes

The questions this part deals with have been partly analysed in [2]. With this aim in view a system with just one population has been analysed, and only the elder stages could attack the younger ones. Some results of this work will be represented without great changes. However, most of them will be essentially generalized and completed and proved by other methods.

Further we will use following terminology.

Definition: Let $x = x(t)$ be a function.

1. We call x asymptotically bounded if constants $C < \infty$ and $t_0 < \infty$ exist, such that $|x(t)| \leq C$ is satisfied for all $t > t_0$.
2. We call x infinitely high if $\lim x(t) = +\infty$ for $t \rightarrow +\infty$.
3. x is vanishing if $\lim x(t) = 0$ for $t \rightarrow +\infty$.
4. x is recurrently bounded if a constant C , $C < \infty$, and a sequence t_i exist, such that $t_i \rightarrow +\infty$ and $|x(t_i)| \leq C$.
5. x is recurrently vanishing if a sequence t_i exists, such that $t_i \rightarrow +\infty$ and $x(t_i) \rightarrow 0$.
6. x is permanent if constants $C > 0$ and $t_0 < \infty$ exist, such that $x(t) \geq C$ is satisfied for all $t \geq t_0$.

We examine a system with a free number of populations. The directions of trophical relations are not restricted, unless it is not explicitly emphasized. The system of differential equations has the form

$$\begin{aligned}
 x'_1 &= -\sigma_{11}x_1 + \sigma_{12}x_2 + \cdots + \sigma_{1n}x_n - x_1 \sum_j f_{1j}x_j \\
 x'_2 &= \sigma_{21}x_1 - \sigma_{22}x_2 - x_2 \sum_j f_{2j}x_j \\
 &\vdots \\
 x'_n &= \sigma_{nn-1}x_{n-1} - \sigma_{nn}x_n - x_n \sum_j f_{nj}x_j. \\
 x'_{n+1} &= -\sigma_{n+1n+1}x_{n+1} + \sigma_{n+1n+2}x_{n+2} + \cdots + \sigma_{n+1n+m}x_{n+m} - x_{n+1} \sum_j f_{n+1j}x_j \\
 &\vdots
 \end{aligned} \tag{1}$$

Further x_1, \dots, x_n are the age stages of the first population, the stages x_{n+1}, \dots belong to the other populations of the system, A is the Leslie-

matrix of the first population,

$$A = \begin{pmatrix} -\sigma_{11} & \sigma_{12} & \sigma_{13} & \cdots & \sigma_{1n} \\ \sigma_{21} & -\sigma_{22} & 0 & \cdots & 0 \\ 0 & \sigma_{32} & -\sigma_{33} & 0 & \cdots \\ & & \ddots & \ddots & \\ 0 & \cdots & 0 & \sigma_{nn-1} & -\sigma_{nn} \end{pmatrix}.$$

A depends on $X_n = (x_1, \dots, x_n)$ and $Y = (x_{n+1}, \dots)$. We write $A(X_n, Y)$ to emphasize, at which point A is calculated. If there are no other populations at all or A does not depend on them, we write $A(X)$.

Let further $A(0_n, \bar{0})$ be this matrix at $X_n = 0_n = (0, \dots, 0)$, $Y = (0, \dots)$. $A(0_n, \infty)$ denotes the limit of A for $X_n = 0_n$ and $x_j \rightarrow \infty$ if $j \geq n+1$. The limit of A is defined by the limits of its elements. Analogously let $A(\infty_n, \bar{\infty})$ be the limit of A for $x_j \rightarrow \infty$, $j \geq 1$. The existence of these limits is obvious.

The terms $\Phi_i(X_n, Y)$ and $\sigma_{ij}(X_n, Y)$ are self-explaining.

Theorem 1. *On the condition $\det(-A(\infty_n, \bar{\infty})) > 0$ $x_1 \cdots, x_n$ are vanishing, i. e. the first population necessarily dies out.*

Proof. Let $q_1 > 0, \dots, q_n > 0$ be the positive constants for $A(\infty_n, \bar{\infty})$ from Lemma 1. Then

$$(q_1 \cdots q_n)A(\infty_n, \bar{\infty}) = (a_1 \cdots a_n), \quad a_1 < 0, \dots, a_n < 0.$$

For any X_n and Y let $(q_1 \cdots q_n)A(X_n, Y) = (b_1 \cdots b_n)$. We estimate the coefficients b_1, \dots, b_n .

If Φ_i depends on X_n or on Y in an untrivial way, then $\Phi_i(\infty_n, \bar{\infty}) = 1$ and hence

$$\begin{aligned} \sigma_{1i}(\infty_n, \bar{\infty}) &= r_i, & \sigma_{ii}(\infty_n, \bar{\infty}) &= w_i, & \sigma_{i+1,i}(\infty_n, \bar{\infty}) &= w_i, \\ a_i &= r_i - q_i w_i + q_{i+1} w_i < 0 & \text{for } 1 < i < n, \\ a_1 &= -w_1 + q_2 w_1 < 0, & a_n &= r_n - q_n w_n < 0. \end{aligned}$$

At the point (X_n, Y) , using the designation $\Phi_i = \Phi_i(X_n, Y)$, $1 \leq i \leq n$, we have

$$b_1 = a_1 \Phi_1 - q_1 m_1 (1 - \Phi_1), \quad b_n = a_n \Phi_n - q_n m_n (1 - \Phi_n)$$

and for $1 < j < n$

$$b_i = q_1 r_i \Phi_i - q_i (w_i \Phi_i + m_i (1 - \Phi_i)) + q_{i+1} w_i \Phi_i = a_i \Phi_i - q_i m_i (1 - \Phi_i).$$

Hence, $b_i \leq c_i = \max\{a_i, -q_i m_i\} < 0$ for $1 \leq i \leq n$.

Otherwise, if Φ_i is independent of X_n and Y , it is merely $b_i = a_i$.

Therefore, we obtain by a linear combination of the first n equations of (1)

$$\begin{aligned} (q_1x_1 + \cdots + q_nx_n)' &= (b_1x_1 + \cdots + b_nx_n) - \sum_{1 \leq i \leq n} q_i x_i \sum_j f_{ij} x_j \\ &\leq (c_1x_1 + \cdots + c_nx_n) < -\alpha(q_1x_1 + \cdots + q_nx_n), \quad \alpha > 0. \end{aligned}$$

Hence,

$$q_1x_1 + \cdots + q_nx_n \leq Ce^{-\alpha t}, \quad q_1x_1 + \cdots + q_nx_n \rightarrow 0,$$

and $x_1 \rightarrow 0, \dots, x_n \rightarrow 0$ for $t \rightarrow \infty$. ■

Theorem 2. *On the condition $\det(-A(0_n, \bar{\infty})) > 0$ a small first population dies out.*

Proof. Let $q_1 > 0, \dots, q_n > 0$ be again the positive constants for $A(0_n, \bar{\infty})$ from lemma 1, such that

$$(q_1 \cdots q_n)A(0_n, \bar{\infty}) = (a_1 \cdots a_n), \quad a_1 < 0, \dots, a_n < 0.$$

Let us estimate the product $(q_1 \cdots q_n)A(X_n, Y) = (b_1 \cdots b_n)$ if X_n lies near 0_n .

If Φ_i depends on Y in an untrivial way, then $\Phi_i(X_n, \bar{\infty}) = 1$,

$$\sigma_{1i}(X_n, \bar{\infty}) = r_i, \quad \sigma_{ii}(X_n, \bar{\infty}) = w_i, \quad \sigma_{i+1,i}(X_n, \bar{\infty}) = w_i,$$

and for any X_n and Y we obtain as before with $\Phi_i = \Phi_i(X_n, Y)$

$$b_i = a_i \Phi_i - q_i m_i (1 - \Phi_i) \leq c_i, \quad c_i = \max\{a_i, -q_i m_i\} < 0.$$

Otherwise both Φ_i and, consequently, b_i are continuous functions of only X_n . Then, obviously, $b_i \rightarrow a_i$ for $X_n \rightarrow 0_n$, and for $|X_n| < \epsilon$ with $\epsilon > 0$ sufficiently small it is $b_i < 0.5a_i$. By a linear combination of the first n equations of (1) we obtain in case $|X_n| < \epsilon$ for small $\epsilon > 0$ and $d_i = \min\{c_i, 0.5a_i\}$, $1 \leq i \leq n$,

$$\begin{aligned} (q_1x_1 + \cdots + q_nx_n)' &< (b_1x_1 + \cdots + b_nx_n) - \sum_{1 \leq i \leq n} q_i x_i \sum_j f_{ij} x_j \\ &< (d_1x_1 + \cdots + d_nx_n) < -\alpha(q_1x_1 + \cdots + q_nx_n), \end{aligned} \tag{2}$$

where $a > 0$.

If for $t = 0$ $x_1(t), \dots, x_n(t)$ are sufficiently small, the tetrahedron

$$q_1x_1 + \cdots + q_nx_n \leq q_1x_1(0) + \cdots + q_nx_n(0), \quad x_1 \geq 0, \dots, x_n \geq 0,$$

is situated within the sphere $|X_n| \leq \epsilon$. Then the inequality also holds for all $t > 0$, and from this it follows again that

$$q_1x_1 + \cdots + q_nx_n \leq Ce^{-\alpha t}, \quad x_1 \rightarrow 0, \dots, x_n \rightarrow 0 \text{ for } t \rightarrow \infty. \quad \blacksquare$$

Remarks. The age stages x_i , $1 \leq i \leq s(A(\infty_n, \bar{\infty}))$, are always necessary for the population's survival. The population would necessarily die out if one of these stages were constantly eliminated.

The stages x_i , $1 \leq i \leq s(A(0_n, \bar{\infty}))$, are necessary for a small population to survive.

For a system with just a single population the theorems 1 and 2 mean respectively that the origin is globally and locally attractive.

Lemma 3. *If the age stage x_i is asymptotically bounded, then its successor stage x_{i+1} in the same population also is asymptotically bounded.*

If x_i is vanishing, then x_{i+1} is vanishing, too.

Proof. Let $x_i < C$ for $t \geq 0$. Then we obtain from the (i+1)-th equation of (1)

$$x'_{i+1} = \sigma_{i+1}x_i - \sigma_{i+1}x_{i+1} - x_{i+1} \sum_j f_{i+1j}x_j \leq MC - \alpha x_{i+1}$$

with

$$M = \max \sigma_{i+1} \leq w_i < \infty, \quad \alpha = \min \sigma_{i+1} \geq \min \{w_{i+1}, m_{i+1}\} > 0.$$

Then for $t > t_0$

$$x_{i+1} \leq \frac{MC}{\alpha} + Ke^{-\alpha(t-t_0)}, \text{ and for sufficient large } t \text{ holds } x_{i+1} \leq \frac{2MC}{\alpha}. \blacksquare$$

The idea of proof for the following lemma is largely taken from [2].

Lemma 4. *Let x_1, \dots, x_k be the first population's age stages which are not attacked by all other stages x_{k+1}, \dots , and within this group let the stages only be attacked by the elder ones. If x_k is recurrently bounded, then the sum $x_1 + \dots + x_k$ is also recurrently bounded. If x_k is recurrently vanishing, then $x_1 + \dots + x_k$ is recurrently vanishing, too.*

Proof. Let $S_k = x_k$, $S_{k-1} = x_{k-1} + x_k$, \dots , $S_1 = x_1 + \dots + x_k$. We start with the proposition's first part. Thus, S_k is recurrently bounded. If $S_i = x_i + \dots + x_k$ is recurrently bounded for $i < k$, then it is obvious that for any $\epsilon > 0$ a constant $C_i < \infty$ and a sequence t_ν , $\nu \geq 1$, do exist, such that $t_\nu \rightarrow +\infty$ and $S_i(t_\nu) \leq C_i$, $S'_i(t_\nu) \leq \epsilon$ hold for any $\nu \geq 1$. $S'_i(t)$ is the derivative of $S_i(t)$.

From (1) we obtain as the sum of the suitable equations

$$\begin{aligned} S'_i &= x'_i + \dots + x'_k = w_{i-1}\Phi_{i-1}x_{i-1} - m_i(1 - \Phi_i)x_i - \dots - m_k(1 - \Phi_k)x_k - \\ &\quad - x_i \sum_{i \leq j \leq k} f_{ij}x_j - x_{i+1} \sum_{i+1 \leq j \leq k} f_{i+1j}x_j - \dots - x_k f_{kk}x_k. \end{aligned}$$

This leads to $x_{i-1}(t_\nu) \leq L_{i-1}$ for sufficiently large ν with

$$L_{i-1} = \frac{1}{w_{i-1}\Phi_{i-1}(0_n, \bar{0})} \left\{ \epsilon + \sum_{i \leq p \leq k} C_p (m_p + \sum_{i \leq j \leq k} f_{pj} C_j) \right\}.$$

Then $S_{i-1}(t_\nu) \leq C_{i-1} = L_{i-1} + C_i < \infty$, $j \geq 1$, i.e. S_{i-1} is recurrently bounded.

In the second case t_ν can be chosen so, that $S_i(t_\nu) \rightarrow 0$, and $S'_i(t_\nu) \rightarrow 0$ for $\nu \rightarrow \infty$. $x_{i-1}(t_\nu) \rightarrow 0$ can be derived from $S_i(t_\nu) \rightarrow 0$ by estimations which are analogous to the last ones. Then S_{i-1} is recurrently vanishing. ■

Remark. If the upper bound C for the asymptotical boundedness can be chosen regardless of the initial conditions for the system of differential equations, there is a global asymptotical boundedness. The global recurrent boundedness can be defined in an analogous way. It is easy to see in the proofs that the lemmas 3 and 4 are also valid for global estimations.

Theorem 3. Let $A = A(0_n, \bar{0})$, $\det(-A) < 0$ and let none of the first $s = s(A)$ age stages be an object of the trophic relations in the system. If in the beginning there is at least one of the first $m = m(A)$ age stages, then x_1, \dots, x_s increase unboundedly.

Proof. Let $q_1 > 0, \dots, q_s > 0$ again be the corresponding constants for A from lemma 1. Then

$$(q_1 \cdots q_s 0 \cdots 0)A(0_n, \bar{0}) = (a_1 \cdots a_n), \quad a_1 > 0, \dots, a_s > 0, a_{s+1} \geq 0, \dots, a_n \geq 0.$$

Let $\Phi_i = \Phi_i(X_n, Y)$ for any X_n and Y , and

$$(b_1 \cdots b_n) = (q_1 \cdots q_s 0 \cdots 0)A(X_n, Y).$$

It is obvious here that

$$\begin{aligned} b_1 &= -q_1 m_1 + [-q_1 w_1 + q_1 m_1 + q_2 w_1] \Phi_1, \\ b_i &= -q_i m_i + [q_1 r_i - q_i w_i + q_i m_i + q_{i+1} w_i] \Phi_i, \quad 2 \leq i \leq s-1, \\ b_s &= -q_s m_s + [q_1 r_s - q_s w_s + q_s m_s] \Phi_s, \\ b_i &= r_i \Phi_i, \quad i > s. \end{aligned}$$

Due to $a_1 > 0, \dots, a_s > 0$ and $-q_i m_i < 0$ the terms in square brackets are positive and it can be seen that all coefficients b_i grow monotonously if Φ_i increases. Since $\Phi_i(X_n, Y) \geq \Phi_i(0_n, \bar{0})$, we have

$$b_1 \geq a_1, \dots, b_s \geq a_s, \quad b_{s+1} \geq 0, \dots, b_n \geq 0.$$

Because there is at least one of the first $m(A)$ age stages, a moment exists when not all reproductive age stages equal 0. At this moment $x_1 > 0$ or $x'_1 > 0$ and x_1 grows. Therefore, we can assume that $q_1x_1 + \dots + q_sx_s = C$, $C > 0$ holds at the moment $t = 0$.

By means of linear combinations of the first s equations of (1) we obtain

$$\begin{aligned} (q_1x_1 + \dots + q_sx_s)' &= b_1x_1 + \dots + b_nx_n \geq a_1x_1 + \dots + a_sx_s \\ &\geq \alpha(q_1x_1 + \dots + q_sx_s), \text{ where } \alpha > 0. \end{aligned}$$

Hence,

$$q_1x_1 + \dots + q_sx_s \geq Ce^{\alpha t}, \quad q_1x_1 + \dots + q_sx_s \rightarrow \infty \text{ for } t \rightarrow \infty. \quad (3)$$

Now we show that all x_i , $1 \leq i \leq s$, are infinitely high. It is true for x_s , because otherwise, according to lemma 4, the sum $x_1 + \dots + x_s$ would have been recurrently bounded as well as x_s , which would have contradicted (3).

From the first equation of (1) it follows

$$x'_1 \geq -\sigma_{11}x_1 + \sigma_{1s}x_s \geq -\alpha x_1 + f(t)$$

with $\alpha = \max \sigma_{11} = \max \{w_1, m_1\}$, $f(t) = \min \sigma_{1s}x_s = r_s\Phi_s(0_n, \bar{0})x_s(t)$, $\Phi_s(0_n, \bar{0}) > 0$. Then $f(t) \rightarrow \infty$ for $t \rightarrow \infty$, and hence

$$x_1(t) \geq Ce^{-\alpha t} + \int_0^t e^{-\alpha(t-u)} f(u) du \rightarrow \infty \text{ for } t \rightarrow \infty.$$

The sum $x_1 + \dots + x_k$, $1 \leq k \leq s$, is infinitely high, and so, according to lemma 4, x_k must also be infinitely high. ■

For a system with an only one population this theorem means that the origin is unstable.

Theorem 4. *Let $A = A(0_n, \bar{0})$, $\det(-A) < 0$, and let none of the first $s = s(A)$ age stages be attacked by the stages of all other populations.*

1. *If in the beginning there is at least one of the first $m = m(A)$ age stages, then at least the youngest reproductive age stage is not vanishing.*

2. *If, furthermore, x_1, \dots, x_s are attacked only by reproductive elder stages, then $x_1 + \dots + x_s$ is permanent.*

Proof. Analogously to the proof of theorem 3 we obtain with $q_1 > 0, \dots, q_s > 0$ the inequality

$$\begin{aligned} (q_1x_1 + \dots + q_sx_s)' &\geq a_1x_1 + \dots + a_sx_s - \\ &-x_1 \sum_{1 \leq j \leq n} f_{1j}x_j - \dots - x_s \sum_{1 \leq j \leq n} f_{sj}x_j. \end{aligned} \quad (4)$$

Let the youngest reproductive stage be vanishing. According to lemma 3 this implies that all reproductive stages of the first population are vanishing. Then one can easily see that x_1 is vanishing, too. Therefore all x_1, \dots, x_n vanish. For large t we obtain the following estimations

$$\sum_{1 \leq j \leq n} f_{ij} x_j < \frac{a_i}{2}, \text{ for every } i, \quad 1 \leq i \leq s,$$

$$(q_1 x_1 + \dots + q_s x_s)' \geq \frac{a_1}{2} x_1 + \dots + \frac{a_s}{2} x_s \geq \alpha (q_1 x_1 + \dots + q_s x_s) \text{ with } \alpha > 0.$$

Hence, $q_1 x_1 + \dots + q_s x_s \rightarrow \infty$, and we come to a contradiction. Thus, the youngest reproductive age stage is not vanishing.

Now let every x_j , $s+1 \leq j \leq n$, be reproductive, if x_j attacks any of the stages x_1, \dots, x_s . In this case (4) can be replaced exacter as follows

$$(q_1 x_1 + \dots + q_s x_s)' \geq a_1 x_1 + \dots + a_s x_s + \sigma_{1s+1} x_{s+1} + \dots + \sigma_{1m} x_m -$$

$$- x_1 \sum_{1 \leq j \leq n} f_{1j} x_j - \dots - x_s \sum_{1 \leq j \leq n} f_{sj} x_j.$$

For $p > s$ we obtain $\sigma_{1p} \geq a_p = r_p \Phi_p(0_n, \bar{0}) > 0$ if $f_{ip} > 0$ holds for any i , $i \leq s$. A simple transformation leads to

$$x_1 \sum_{1 \leq j \leq n} f_{1j} x_j + \dots + x_s \sum_{1 \leq j \leq n} f_{sj} x_j = x_1 \sum_{1 \leq j \leq s} f_{1j} x_j + \dots + x_s \sum_{1 \leq j \leq s} f_{sj} x_j$$

$$+ x_{s+1} \sum_{j < s} f_{js+1} x_j + \dots + x_n \sum_{j < s} f_{jn} x_j.$$

We can choose $\delta > 0$ so small that $q_1 x_1 + \dots + q_s x_s < \delta$ implies

$$\sum_{1 \leq j \leq s} f_{1j} x_j \leq \frac{a_1}{2}, \quad \dots, \quad \sum_{1 \leq j \leq s} f_{sj} x_j \leq \frac{a_s}{2},$$

$$\sum_{1 \leq j \leq s} f_{js+1} x_j \leq \frac{a_{s+1}}{2}, \quad \dots, \quad \sum_{1 \leq j \leq s} f_{jn} x_j \leq \frac{a_n}{2}.$$

Then, for $q_1 x_1 + \dots + q_s x_s < \delta$,

$$(q_1 x_1 + \dots + q_s x_s)' \geq \frac{a_1}{2} x_1 + \dots + \frac{a_s}{2} x_s \geq \alpha (q_1 x_1 + \dots + q_s x_s) \text{ with } \alpha > 0.$$

Hence, $q_1 x_1 + \dots + q_s x_s \geq \delta$ holds for large t , and the sum $x_1 + \dots + x_s$ is permanent. ■

By means of some exacter estimations we can also find a lower bound of permanency for $x_1 + \dots + x_s$.

In the following theorems we assume that in the system there is only one population with n age stages x_1, \dots, x_n where only the elder stages can attack the younger ones, i. e. $f_{ij} = 0$ for $i \geq j$.

Theorem 5. *For the Leslie-matrix $A = A(\infty_n)$ let $\det(-A) < 0$, $s = s(A)$, $m = m(A)$ and let x_p be the eldest stage that attacks another one which is always necessary.*

1. *If x_1, \dots, x_p are not attacked by x_{p+1}, \dots, x_n and for $p < m$ the stages x_1, \dots, x_m are also not attacked by x_{m+1}, \dots, x_n , then the whole population is asymptotically bounded.*

2. *If furthermore $\det(-A(0_n)) < 0$ and in the beginning there is at least one of the age stages x_1, \dots, x_m , then $x_1 + \dots + x_s$ is permanent.*

Proof. Let x_k be the always necessary stage, which is attacked by x_p , i. e. $k \leq s$ and $f_{kp} > 0$. Let us denote $\nu = \max\{p, m\}$, so that x_1, \dots, x_ν do not depend on $x_{\nu+1}, \dots, x_n$.

First we remark that the stage x_p is recurrently bounded. Indeed, let q_1, \dots, q_m be the coefficients from lemma 2. Then

$$(q_1 \cdots q_m 0 \cdots 0)A = (0 \cdots 0 c_k 0 \cdots 0),$$

and at any point X_n it holds that

$$(q_1 x_1 + \cdots + q_m x_m)' = \sum_{1 \leq i \leq m} b_i x_i - \sum_{1 \leq i \leq m} q_i x_i \sum_{i < j \leq n} f_{ij} x_j$$

with $b_i \leq 0$ for $i \neq k$ and $b_k \leq c_k$.

Thus, we have

$$(q_1 x_1 + \cdots + q_m x_m)' < x_k (c_k - q_p f_{kp} x_p),$$

and x_p cannot be infinitely high because $x_p > a_k / q_p f_{kp}$ implies $(q_1 x_1 + \cdots + q_m x_m)' < 0$. This means that x_1 and all other age stages are bounded. So x_p is recurrently bounded, and, according to lemma 4, the sum $x_1 + \cdots + x_p$ is recurrently bounded, too.

Now let us show that $x_1 + \cdots + x_\nu$ is recurrently bounded. In the case $p \geq m$ it is clear, and hence, we assume $p < m = \nu$. In this case there are $C < \infty$ and $t_l, t_l \rightarrow \infty$, such that in the points t_l the following conditions are satisfied: $x_1 + \cdots + x_p \leq C$ and $(x_1 + \cdots + x_p)' \leq 1$. From the system's first p equations follows

$$(x_1 + \cdots + x_p)' \geq - \sum_{1 \leq i \leq p} (w_i + m_i) x_i - \sum_{1 \leq i \leq p-1} x_i \sum_{1 \leq j \leq p} f_{ij} x_j + M_m x_m \quad (5)$$

with $M_m = r_m \Phi_m(0_n) > 0$. Now the recurrent boundedness of x_m can be easily derived from (5). By means of lemma 4 we obtain that $x_1 + \dots + x_m$ is recurrently bounded as well.

Further, let C denote the corresponding upper bound for $x_1 + \dots + x_\nu$. Since x_1, \dots, x_ν are independent of $x_{\nu+1}, \dots, x_n$, we consider the part of the system of differential equations for x_1, \dots, x_ν . From the last it follows that every orbit necessarily reaches into the tetrahedron

$$K = \{(x_1, \dots, x_\nu) : x_1 + \dots + x_\nu \leq C, \quad x_1 \geq 0, \dots, x_\nu \geq 0\}$$

Let $X_\nu = (x_1, \dots, x_\nu)$ be a boundary point of K , where $x_1 + \dots + x_\nu = C$ is satisfied. In this case we define a function $F(X_\nu)$ as follows:

$F(X_\nu) = C$ if the orbit starting in X_ν goes into the tetrahedron,

$F(X_\nu) = \max\{x_1(t) + \dots + x_\nu(t), 0 \leq t \leq T\}$ if the orbit leaves the tetrahedron at the instant $t = 0$ and comes back into there for the first time at the moment T .

X_ν determines the initial conditions for the system of differential equations and $F(X_\nu)$, obviously, is a continuous function of X_ν . Then $F(X_\nu)$ is bounded above at the compact $\{(x_1, \dots, x_\nu) : x_1 + \dots + x_\nu = C, x_1 \geq 0, \dots, x_\nu \geq 0\}$. I.e. $x_1 + \dots + x_\nu$ is asymptotically bounded. The asymptotical boundedness of $x_{\nu+1}, \dots, x_n$ follows from lemma 3.

Finally, we show the permanence of $x_1 + \dots + x_s$. As in the proof of theorem 4 there exist $\delta > 0$, such that the projection (x_1, \dots, x_s) of every orbit (x_1, \dots, x_n) leaves necessarily the tetrahedron

$$K_\delta = \{(x_1, \dots, x_s) : x_1 + \dots + x_s \leq \delta, \quad x_1 \geq 0, \dots, x_s \geq 0\}$$

if there is one of the stages x_1, \dots, x_m . We can assume that $x_1(0) > 0$, because otherwise $x_1(t) > 0$ holds for some $t > 0$, and we need just to make a shift of time. Let $X_s = (x_1, \dots, x_s)$, so that for $t = 0$ the condition $x_1(0) + \dots + x_s(0) = \delta > 0$ is satisfied. Let $Y = (x_{s+1}, \dots, x_n)$ be freely choosable. We define $G(X_s, Y)$ as follows:

$G(X_s, Y) = \delta$ if the projection (x_1, \dots, x_s) of the orbit starting in (X_s, Y) leaves the tetrahedron K_δ ,

$G(X_s, Y) = \min\{x_1(t) + \dots + x_s(t), 0 \leq t \leq T\}$ if the orbit reaches into this tetrahedron at $t = 0$ and leaves it for the first time at $t = T$, $T > 0$. The function $G(X_s, Y)$ is continuous, and for X_s and Y are varied on the compacts, it reaches its minimum. This minimum is positive because x_1 is not vanishing and is a lower bound in the permanence condition. ■

Remark. From the last proof and the remark on lemma 3 it can easily be deduced that in the first case the whole population is indeed globally

asymptotically bounded. The lower bound of permanence in the second part also has a global character.

The next two theorems give other sufficient boundedness conditions. The first theorem is taken over from [2].

Theorem 6. *If every reproductive age stage is cannibalistic regarding the youngest one, then the population is asymptotically bounded.*

Proof. From the first equation of (1) we obtain

$$x_1' \leq -\sigma_{11}x_1 + \sum_{1 \leq j \leq n} x_j(\sigma_{1j} - f_{1j}x_1) \leq -\sigma_{11}x_1 + \sum_{1 \leq j \leq n} x_j(r_j - f_{1j}x_1).$$

For $x_1 > \max r_j/f_{1j}$ this yields $x_1' < 0$, and therefore x_1 is asymptotically bounded. ■

Definition. *The function $x(t)$ is bounded on average, if a constant C , $C < \infty$, exists, such that for $t > 0$*

$$\frac{1}{t} \left| \int_0^t x(u) du \right| \leq C.$$

Theorem 7. *If the age stage x_k is bounded on average, then all the next ones are bounded on average, too. If in this case x_1, \dots, x_k are attacked only by the elder stages, then the whole population is asymptotically bounded.*

Proof. We show that average boundedness of x_k implies average boundedness of x_{k+1} . Let C_k be a finite bound of x_k . The x_{k+1} -th differential equation from (1) is

$$x_{k+1}' = \sigma_{k+1k}x_k - \sigma_{k+1k+1}x_{k+1} - x_{k+1} \sum_j f_{k+1j}x_j.$$

We come immediately to

$$|x_{k+1}'| \leq \sigma_{k+1k}x_k, \quad x_{k+1} \leq \frac{2\sigma_{k+1k}}{\sigma_{k+1k+1}}x_k$$

and therefore

$$\frac{1}{t} \left| \int_0^t x_{k+1}(u) du \right| \leq C_{k+1} \text{ with } C_{k+1} = \frac{2w_k C_k}{\min\{w_{k+1}, m_{k+1}\}} < \infty.$$

Thus, the age stages x_k, x_{k+1}, \dots, x_n and, hence, their sum $S_k = x_k + \dots + x_n$ are bounded on average. With $C < \infty$ we have

$$\frac{1}{t} \left| \int_0^t S_k(u) du \right| \leq C.$$

We define the subset of $[0, t]$

$$\mathcal{K}(t, 2C) = \{u : 0 \leq u \leq t, S_k(u) \leq 2C\}.$$

The last inequality for the integral implies that the measure μ of $\mathcal{K}(t, 2C)$ satisfies $\mu(\mathcal{K}(t, 2C)) \geq 0.5t$. Hence, on the interval $[0, t]$ there are many points u , such that $S_k(u) \leq 2C$. This implies particularly that the sum S_k is recurrently bounded.

Indeed, let $t > 0$. Then $\mathcal{K}(6t, 2C)$ satisfies $\mu(\mathcal{K}(6t, 2C)) \geq 3t$, $\mathcal{K}(6t, 2C) \not\subseteq [0, 2t]$ and hence, $\mathcal{K}(6t, 2C) \cap [2t, 6t] \neq \emptyset$. Thus, for every t , $0 < t < \infty$, there is t_0 , $t_0 > 2t$, such that $S_k(t_0) \leq 2C$. Therefore, an infinite sequence t_i , $t_i \rightarrow \infty$, obviously exists, such that $S_k(t_i) \leq 2C$.

As before in the proof of lemma 4, it can be easily be shown that all sums $S_i = x_1 + \dots + x_n$, $i \leq k$, are recurrently bounded. The asymptotical boundedness can be followed in the same way as in theorem 5. ■

4 Stationary points

In the next two theorems the question of existence and uniqueness of nontrivial stationary points is analysed. In this context the following is remarkable. For an asymptotically bounded system the existence of a stationary point can be proved by means of Brouwer's theorem, [1,17]. Nevertheless, since we do not assume the boundedness and emphasize the uniqueness, another way of proof is chosen.

Theorem 8. *Let the Leslie-matrix of the system be constant and the origin instable. If the youngest stage of prey x_u is always necessary for the survival, then exactly one nontrivial stationary point exists.*

Proof. The instability of the origin is equivalent to $\Delta = \det(-A) < 0$, and the stage x_u is always necessary for the survival if $\Delta_{u-1} = \det(-A_{u-1}) > 0$ holds.

For a stationary point we have

$$\begin{aligned} -\sigma_{11}x_1 + \sigma_{12}x_2 + \dots + \sigma_{1n}x_n - x_1 \sum_{j>1} f_{1j}x_j &= 0 \\ \vdots & \\ \sigma_{ii-1}x_{i-1} - \sigma_{ii}x_i - x_i \sum_{j>i} f_{ij}x_j &= 0 \\ \vdots & \\ \sigma_{nn-1}x_{n-1} - \sigma_{nn}x_n &= 0. \end{aligned} \tag{6}$$

Let $x_n = z$ and $p_n = 1$, so that $x_n = zp_n$. Beginning with it, we want to write in turn x_{n-1}, \dots, x_1 in the form $x_i = zp_i$, where p_i is a polynomial.

From the last equation of (6) follows

$$x_{n-1} = x_n \frac{\sigma_{nn}}{\sigma_{nn-1}} = zp_n \frac{\sigma_{nn}}{\sigma_{nn-1}} = zp_{n-1} \text{ with } p_{n-1} = p_n \frac{\sigma_{nn}}{\sigma_{nn-1}}$$

and for x_{i-1} we obtain from the i -th equation, $i < n$,

$$\begin{aligned} x_{i-1} &= x_i \left(\frac{\sigma_{ii}}{\sigma_{ii-1}} + \sum_{j>i} \frac{f_{ij}}{\sigma_{ii-1}} x_j \right) = zp_i \left(\frac{\sigma_{ii}}{\sigma_{ii-1}} + z \sum_{j>i} \frac{f_{ij}}{\sigma_{ii-1}} p_j \right) = zp_{i-1}, \\ p_{i-1} &= p_i \left(\frac{\sigma_{ii}}{\sigma_{ii-1}} + z \sum_{j>i} \frac{f_{ij}}{\sigma_{ii-1}} p_j \right). \end{aligned}$$

For any polynomial p let $\deg(p)$, $LC(p)$, $CT(p)$ denote the degree, the leading coefficient and the constant term respectively. From the definition of p_n, \dots, p_1 we obtain easily that these are polynomials with nonnegative coefficients. It is obvious that

$$\deg(p_{i-1}) \geq \deg(p_i), \text{ and } \deg(p_{i-1}) = \deg(p_i) \Leftrightarrow \sum_{j>i} f_{ij} = 0.$$

This means that x_i is no stage of prey. Substituting x_1, \dots, x_n into the first equation of (6) we obtain an equation $p(z) = 0$, if $z \neq 0$. $p = p(z)$ is the following polynomial

$$p(z) = -\sigma_{11}p_1 + \sigma_{12}p_2 + \dots + \sigma_{1n}p_n - zp_1 \sum_{j>1} f_{1j}p_j.$$

We calculate the sign of $LC(p)$ and $CT(p)$. For the youngest stage x_u let $u > 1$. Then

$$\begin{aligned} \deg(p_{u-1}) &= \dots = \deg(p_1), \\ a = LC(p_{u-1}) &> 0, LC(p_{u-2}) = \frac{\sigma_{u-1u-1}}{\sigma_{u-1u-2}}a, \dots, LC(p_1) = \frac{\sigma_{22} \dots \sigma_{u-1u-1}}{\sigma_{21} \dots \sigma_{u-1u-2}}a. \end{aligned}$$

From this we obtain easily

$$\begin{aligned} LC(p) &= -\sigma_{11} \frac{\sigma_{22} \dots \sigma_{u-1u-1}}{\sigma_{21} \dots \sigma_{u-1u-2}}a + \sigma_{12} \frac{\sigma_{33} \dots \sigma_{u-1u-1}}{\sigma_{32} \dots \sigma_{u-1u-2}}a + \dots + \sigma_{1u-1}a = \\ &= \frac{-\Delta_{u-1}}{\sigma_{21} \dots \sigma_{u-1u-2}}a = a_0 < 0. \end{aligned}$$

Also if x_1 is the youngest stage of prey, there is still

$$LC(p) = -LC(p_1)LC\left(\sum_{j>1} f_{1j}p_j\right) = a_0 < 0.$$

The constant terms obviously satisfy

$$CT(p_n) = 1, CT(p_{i-1}) = \frac{\sigma_{ii} \cdots \sigma_{nn}}{\sigma_{ii-1} \cdots \sigma_{nn-1}} \text{ for } 1 < i \leq n$$

and therefore

$$CT(p) = -\sigma_{11} \frac{\sigma_{22} \cdots \sigma_{nn}}{\sigma_{21} \cdots \sigma_{nn-1}} + \sigma_{12} \frac{\sigma_{33} \cdots \sigma_{nn}}{\sigma_{32} \cdots \sigma_{nn-1}} + \cdots + \sigma_{1n} = \frac{-\Delta}{\sigma_{21} \cdots \sigma_{nn-1}} = a_k > 0.$$

Thus, the polynomial $p(z)$ has the form

$$p(z) = a_0 z^k + a_1 z^{k-1} + \cdots + a_k, \text{ with } a_0 < 0, a_k > 0.$$

Then an untrivial solution \bar{z} of the equation $p(z) = 0$ exists, and \bar{z} determines, obviously, an untrivial stationary point $(\bar{x}_1, \cdots, \bar{x}_n)$. Now we must show that this stationary point is the only one.

Since the coefficients of $p_i(z)$ are nonnegative, $p_i(z)$ grows monotonously, if $z, z > 0$, increases. Then the representation $x_i = zp_i(z)$ yields that all the coordinates x_i grow monotonously if the last coordinate $x_n = z$ increases. Let $(\bar{x}_1, \cdots, \bar{x}_n)$ be the stationary point with the smallest coordinates and $x_i = y_i + \bar{x}_i, 1 \leq i \leq n$. For the new variables $y_i, 1 \leq i \leq n$, we have

$$\begin{aligned} y'_1 &= -\sigma_{11}(y_1 + \bar{x}_1) + \sum_{2 \leq j \leq n} \sigma_{1j}(y_j + \bar{x}_j) - \sum_{j>1} f_{1j}(y_1 + \bar{x}_1)(y_j + \bar{x}_j) \\ &= -(\sigma_{11} + \sum_{j>1} f_{1j}\bar{x}_j)y_1 + \sigma_{12}y_2 + \cdots + \sigma_{1n}y_n - \sum_{j>1} f_{1j}(y_1 + \bar{x}_1)y_j + \\ &\quad [-\sigma_{11}\bar{x}_1 + \sigma_{12}\bar{x}_2 + \cdots + \sigma_{1n}\bar{x}_n - \sum_{j>1} f_{1j}\bar{x}_1\bar{x}_j] \\ &= -\bar{\sigma}_{11}y_1 + \sigma_{12}y_2 + \cdots + \sigma_{1n}y_n - \sum_{j>1} f_{1j}(y_1 + \bar{x}_1)y_j, \quad \bar{\sigma}_{11} = \sigma_{11} + \sum_{j>1} f_{1j}\bar{x}_j. \end{aligned}$$

The term in square brackets equals 0 here. Analogously we obtain for $i > 1$

$$y'_i = \sigma_{ii-1}y_{i-1} - \bar{\sigma}_{ii}y_i - \sum_{j>i} f_{ij}(y_i + \bar{x}_i)y_j \text{ with } \bar{\sigma}_{ii} = \sigma_{ii} + \sum_{j>i} f_{ij}\bar{x}_j.$$

Finally, we come to the system

$$\begin{aligned} y'_1 &= -\bar{\sigma}_{11}y_1 + \sigma_{12}y_2 + \cdots + \sigma_{1n}y_n - (\bar{x}_1 + y_1) \sum_{j>1} f_{1j}y_j \\ &\vdots \\ y'_i &= \sigma_{ii-1}y_{i-1} - \bar{\sigma}_{ii}y_i - (\bar{x}_i + y_i) \sum_{j>i} f_{ij}y_j \\ &\vdots \\ y'_n &= \sigma_{nn-1}y_{n-1} - \sigma_{nn}y_n. \end{aligned} \tag{7}$$

If \bar{A} is the Leslie-matrix of the system (7), then at the origin $\bar{Y}_0 = (y_1, \dots, y_n) = (0, \dots, 0)$ we have $\det \bar{A}(\bar{Y}_0) = 0$. This follows from the fact that $\bar{X} = (\bar{x}_1, \dots, \bar{x}_n)^T$ is an untrivial solution of the linear system $\bar{A}(\bar{Y}_0)\bar{X} = 0$.

Let m be the eldest reproductive age stage. Then, obviously, $\det \bar{A}_m = \det \bar{A}(\bar{Y}_0) = 0$ and $\det(-\bar{A}_{m-1}) > 0$.

According to lemma 4, positive $q_1 > 0, \dots, q_m > 0$ exist, such that

$$(q_1, \dots, q_m, 0, \dots, 0)\bar{A} = (0, \dots, 0).$$

This leads immediately to

$$v' = (q_1 y_1 + \dots + q_m y_m)' = - \sum_{1 \leq i \leq m} q_i (\bar{x}_i + y_i) \sum_{j > i} f_{ij} y_j < 0$$

for $y_1 > 0, \dots, y_n > 0$. Thus, the points (y_1, \dots, y_n) with positive coordinates are not stationary. ■

Remark. In case of a constant Leslie-matrix with $\det A = 0$ it can be immediately shown by estimations, which are analogous to the last ones, that

1) the origin is asymptotically stable if at least one of the reproductive age stages functions as prey.

2) the origin is stable and the population bounded in the other case.

Theorem 9. *Let A be the system's Leslie-matrix. If $\det(-A(0_n)) < 0$ and the youngest stage of prey x_u is always necessary, i. e. $u \leq s(A(\infty_n))$, then an untrivial stationary point does exist.*

Proof. We denote

$$\Phi_{0i} = \Phi_i(0_n) \text{ and } \Phi_{1i} = \Phi_i(\infty_n), \quad 1 \leq i \leq n.$$

In particular, $\Phi_i \equiv \Phi_{0i} = \Phi_{1i}$ is constant if the stage x_i is not predatory. Otherwise, $0 < \Phi_{0i} < \Phi_{1i} = 1$. In this case $\mathcal{K} = [\Phi_{01}, \Phi_{11}] \times \dots \times [\Phi_{0n}, \Phi_{1n}] \subset R^n$ is the state space of the fitness-functions.

Let us determine a constant Leslie-matrix $B = A(\Phi)$ for any value $\Phi \in \mathcal{K}$. The elements of the matrix B are continuous functions of Φ , and B satisfies the conditions of the last theorem. Indeed, $\Phi_0 \leq \Phi$ and $\det(-A(0)) < 0$ yields $\det(-B) = \det A(\Phi) < 0$. Analogously, from $\Phi \leq \Phi_1$ and $\det(-A_{u-1}(\infty)) > 0$ we obtain $\det(-B_{u-1}) > 0$.

For the system of differential equations with B as the Leslie-matrix, and the same coefficients f_{ij} as in the original system, we can define as in the last theorem the polynomials p_1, \dots, p_n and $p(z) = a_0 z^k + a_1 z^{k-1} + \dots + a_k$ with $a_0 < 0$ and $a_k > 0$. It is clear that the coefficients of all polynomials p_1, \dots, p_n, p are continuous functions of Φ .

Since the polynomial $p(z)$ always has exactly one positive root \bar{z} , \bar{z} is a continuous function of the coefficients a_0, \dots, a_k and therefore of Φ , too. The stationary point \bar{X} , corresponding to \bar{z} , is also continuously dependent on Φ . If we calculate the new values of the fitness-function $\bar{\Phi} = (\Phi_1(\bar{X}), \dots, \Phi_n(\bar{X}))$ at the point \bar{X} , we obtain by $F(\Phi) = \bar{\Phi}$ a continuous map $F : \mathcal{K} \rightarrow \mathcal{K}$. According to Brouwer's theorem, [1], F has a fixed point Φ^* . It is clear that the stationary point which is determined as before by Φ^* , is an untrivial stationary point for the system with a nonconstant Leslie-matrix. This completes the proof.

Acknowledgements. We thank the Deutsche Forschungsgemeinschaft for supporting this reserch.

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