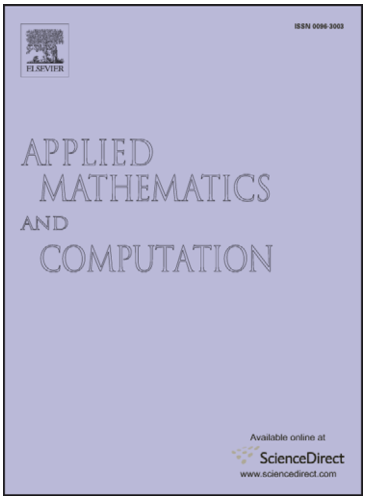

Qualitative behaviour of *n*-dimensional ratio-dependent predator-prey systems

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Qualitative behaviour of n-dimensional ratio-dependent predator-prey systems

by

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Abstract

This paper deals with the qualitative properties of an n-dimensional autonomous system of differential equations, modeling the general ratio-dependent predator-prey interaction.

Key words and phrases: Predator-prey system, Functional response, Sign stability, Ratio dependence

1 Introduction

Let us consider the following ecological system, in which n different predator species are (the i-th predator quantities at time t are denoted by $y_i(t)$, $i = 1, 2, \ldots, n$ respectively) competing for a single prey species (the quantity of prey at time t is denoted by $x(t)$):

$$\left.\begin{array}{rcl} \dot{x} & = & rxg(x,K) - \sum\limits_{i=1}^{n} y_i p_i(x, y_i, a_i) \\ \dot{y}_i & = & y_i p_i(x, y_i, a_i) - d_i y_i, \quad i = 1, 2, \ldots, n \end{array}\right\}, \tag{1}$$

where dot means differentiation with respect to time t. We assume that the per capita growth rate of prey in absence of predators is $rg(x, K)$ where r is a positive constant (in fact the maximal growth rate of prey), $K > 0$ is the carrying capacity of environment with respect to the prey, the function g satisfies the conditions $g \in C^2\left((0,\infty) \times (0,\infty), \mathbb{R}\right)$, $g \in C^0\left([0,\infty) \times (0,\infty), \mathbb{R}\right)$,

$$g(0,K) = 1, \quad g'_x(x,K) < 0 < g''_{xK}(x,K), \quad x > 0, \quad K > 0 \tag{2}$$

$$\lim_{K \to \infty} g'(x,K) = 0 \tag{3}$$

uniformly in $[\delta, x_0]$ for any $0 < \delta < x_0$, and the (possibly) improper integral $\int_0^{x_0} g'_x(x,K)dx$ is uniformly convergent in $[K_0, \infty)$ for any $K_0 > 0$,

$$(K - x)g(x,K) > 0, \quad x \geq 0, \quad K > 0. \tag{4}$$

The so called logistic growth rate of prey

$$g(x,K) = 1 - \frac{x}{K} \tag{5}$$

satisfies the conditions (2)-(4) (cf. [8], [9]).

We assume further that the death rate $d_i > 0$ of predator i is constant and the per capita birth rate of the same predator is $p_i(x, y_i, a_i)$ where the function p_i satisfies the following conditions: $p_i \in C^1((0,\infty)\times(0,\infty),\mathbb{R})$, $p_i \in C^0([0,\infty)\times(0,\infty),\mathbb{R})$,

$$p_i(0, y_i, a_i) = 0, \;\; p'_{ix}(x, y_i, a_i) > 0, \;\; x > 0, \;\; a_i > 0, \tag{6}$$

$$p'_{ix}(x, y_i, a_i) < \frac{p_i(x, y_i, a_i)}{x}, \;\; x > 0, \;\; a_i > 0, \tag{7}$$

$$p'_{ia_i}(x, y_i, a_i) \le 0, \;\; x > o, \;\; a_i > 0. \tag{8}$$

Finally, we assume that the presence of predators decreases the growth rate of prey by the amount equal to the birth rate of the respective predator. The conditions (2)-(4) are the same as those in [8], and conditions (6)-(8) are the generalized case of the per capita birth rate p_i for that case when it depends also on the i-th predator. Thus, we can disregard the detailed interpretation of these conditions. We focus on the function p now. The constant a_i is the "half-saturation constant", namely in the case where p_i is a bounded function for fixed $a_i > 0$, $m_i = \sup\limits_{x,y_i>0} p_i(x, y_i, a_i)$ is the "maximal birth rate" of the i-th predator (m_i can be infinity if p is unbounded). For the survival of predator i it is, clearly, necessary that the maximal birth rate be larger, than the death rate:

$$m_i > d_i. \tag{9}$$

This will be assumed in the sequel.

Let us make an overview of the concrete functions p_i which were used before. The so called Holling II functional response was used in [10]:

$$p_i(x, a_i) = m_i \frac{x}{a_i + x}, \tag{10}$$

the Holling III functional response can be found for example in [11]:

$$p_i(x, a_i) = m_i \frac{x^n}{a_i^n + x^n} \tag{11}$$

and the Ivlev functional response is (cf. [18], [16]):

$$p_i(x, a_i) = m_i \left(1 - e^{-\frac{x}{a_i}}\right). \tag{12}$$

If, in particular, $p_i(x, y_i, a_i) := p_i\left(\frac{y_i}{x}, a_i\right)$ then this case is called a ratio-dependent model. The Michaelis-Menten functional response is, (see for example [14], [20])

$$p_i\left(\frac{y_i}{x}, a_i\right) = m_i \frac{x}{a_i y_i + x}. \tag{13}$$

Analogously, we may write the ratio-dependent Ivlev functional response in the following form:

$$p_i\left(\frac{y_i}{x}, a_i\right) = m_i \left(1 - e^{-\frac{x}{a_i y_i}}\right) \tag{14}$$

which has not been applied yet. Model (1) is called non-degenerate, if the function p_i is given by (10)-(12) according to the fact, that $\left(\frac{p_i(x, a_i)}{p_j(x, a_j)}\right)'_x \neq 0$ if $a_i \neq a_j$ as it was defined in [8]. We may generalize this property in the following way:

Definition 1.1. The ratio-dependent functional response $p_i(\frac{y_i}{x}, a_i)$ is called non-degenerate, if $\left(\frac{p_i\left(\frac{y_i}{x}, a_i\right)}{p_j\left(\frac{y_i}{x}, a_j\right)}\right)'_x \neq 0$ for $a_i y_i \neq a_j y_j$.

Theorem 1.1. *The Michaelis-Menten functional response given by (13) is non-degenerate.*

Proof.

$$p_{i\,x}'\left(\frac{y_i}{x}, a_i\right) p_j\left(\frac{y_j}{x}, a_j\right) - p_{j\,x}'\left(\frac{y_j}{x}, a_j\right) p_i\left(\frac{y_i}{x}, a_i\right)$$

$$= \frac{m_i m_j x^2}{(a_i y_i + x)^2 (a_j y_j + x)^2}(a_i y_i - a_j y_j) \neq 0 \quad (a_i y_i \neq a_j y_j).$$

$\square$

Theorem 1.2. *The ratio-dependent Ivlev functional response given by (14) is non-degenerate.*

Proof.

$$p_{i_x}'\left(\frac{y_i}{x},a_i\right)p_j\left(\frac{y_j}{x},a_j\right)-p_{j_x}'\left(\frac{y_j}{x},a_j\right)p_i\left(\frac{y_i}{x},a_i\right)$$

$$=\frac{m_i m_j}{x}\left(\frac{x}{a_i y_i}e^{-\frac{x}{a_i y_i}}\left(1-e^{-\frac{x}{a_j y_j}}\right)-\frac{x}{a_j y_j}e^{-\frac{x}{a_j y_j}}\left(1-e^{-\frac{x}{a_i y_i}}\right)\right)\neq 0 \quad (a_i y_i \neq a_j y_j),$$

because using the notation $\alpha := \frac{x}{a_i y_i} \neq \frac{x}{a_j y_j} =: \beta$ it is true that $\frac{\alpha e^{-\alpha}}{1-e^{-\alpha}} \neq \frac{\beta e^{-\beta}}{1-e^{-\beta}}$ because the function $f(x) :\equiv \frac{x e^{-x}}{1-e^{-x}}$ is a strictly monotone decreasing function on the non-negative half line. □

Paper [10] deals with the qualitative behavior of system (1) in case of (5) and (10) when $n = 3$. Paper [16] deals with the qualitative behavior of the system (1) in case of (5) and (12) when $n = 3$. The general case of the system (1) can be found in [8] when $n = 3$.

It was shown that the origin, the point $(K, 0, 0)$ and the point E^* (where E^* can be any point of a segment, called a ”zip”) are equilibrium points of the system. In these cases all the points of this segment are stable when K is in an interval, relatively low. If K increases and leaves this interval then the points of the segment are continuously losing the stability starting from an endpoint of the segment to the other one. This process is the zip bifurcation. This is a paradox of enrichment, namely the increasing of the carrying capacity destabilizes the system. One of the predators is called a K-strategist, if it has a relatively low growth rate and may survive with low carrying capacity K. A species is an r-strategist if it has a high growth rate, see in [18], [9]. When $x = a_i$, then the per capita growth rate is half of the maximal. The lower the half saturation constant a_i is, the less prey is needed for the maintenance of the predator. Therefore, a predator with low half saturation constant is a K-strategist. It was shown that as K grew the K-strategist lost ground and only the r-strategist survived with the prey. If the model is degenerated, for example in case of Rosenzweig model, see in [16], the zip bifurcation does not occur. The phenomenon was generalized to a four-dimensional case using (11) see in [11]. This is a so called velcro bifurcation. There are more general results for the $(n+1)$-dimensional case using (10), see in [12]. We note, that these models are structurally unstable, because these systems have zero eigenvalues.

If we use the function (13) we get a ratio-dependent predator-prey system which is capable of producing richer and more reasonable or acceptable dynamics. Originally in [3] it was suggested that the functional response should be expressed in terms of the ratio of prey to predators. A similar feeding equation was proposed previously in [6] (c.f. [4]). There is a growing biological and physiological evidence [1], [2], [7] that in many situations (when competition for food is very sharp), a more suitable general predator-prey theory should be based on the ratio-dependent theory. There are more general cases of ratio-dependence, see in [17]. These ratio-dependent systems are two-dimensional models. There are some results for three-dimensional cases using (13), see in [14], [5], also results for n-dimensional food-chain model in case of (13), see in [21].

Our aim is in this paper to give a survey of the qualitative behavior of the $(n+1)$-dimensional ratio-dependent n predator one prey models. We will show a new class of these models, namely using (14). We will show the common property of the ratio-dependence in the most general non-degenerate case. We will discuss the difference between the general functional response with and without ratio-dependence using the investigation of the graphs of its interaction matrices. We will give sufficient conditions of sign-stability (cf. [15]).

2 The Michaelis-Menten type functional response

2.1 The 3-dimensional case

Let us consider the system (1) in case of (5) and (13). We get:

$$\left.\begin{array}{rcl}\dot{x} & = & rx\left(1-\dfrac{x}{K}\right)-m_1\dfrac{xy_1}{a_1y_1+x}-m_2\dfrac{xy_2}{a_2y_2+x}\\ \dot{y}_1 & = & m_1\dfrac{xy_1}{a_1y_1+x}-d_1y_1\\ \dot{y}_2 & = & m_2\dfrac{xy_2}{a_2y_2+x}-d_2y_2\end{array}\right\}. \tag{15}$$

The domain of definition of (15) is $\{(x, y_1, y_2)|\ x^2+y_1^2>0,\ x^2+y_2^2>0\}$ which can be extended for $\mathbb{R}^3_+=\{(x, y_1, y_2)|\ x\geq 0, y_1\geq 0, y_2\geq 0\}$ by $\dot{x}=0,\ \dot{y}_i=0$ if $x^2+y_i^2=0$ for any i, $i=1,2$. In this case the system is called an extended system of (15). Note, the extended system is continuous on $\mathbb{R}^3_+$. The righthand sides of (15) are smooth functions, therefore the positive octant of the interior of $\mathbb{R}^3_+$ is an invariant region (see [19]).

Lemma 2.1. *The system (15) is dissipative, i.e. all solutions are bounded.*

Proof. Clearly,

$$\dot{x}\leq rx\left(1-\frac{x}{K}\right),$$

implying that

$$\lim_{t\to+\infty}\sup x(t)\leq K.$$

It means that for any $0<\varepsilon<1$, we have $x(t)<K+\varepsilon$ for large t. If we add the three equations of (15) then we have

$$(x+y_1+y_2)^{\cdot}=\dot{x}+\dot{y_1}+\dot{y_2}=rx\left(1-\frac{x}{K}\right)-d_1y_1-d_2y_2,$$

which implies that there exists a constant $C > 0$ such that all trajectories initiated in $\mathbb{R}^3_+$ enter the symplectical region

$$\Omega := \left\{(x, y_1, y_2) \in \mathbb{R}^3_+ | \ x + y_1 + y_2 \leq C + \varepsilon \text{ for any } \varepsilon > 0\right\}.$$

□

The extended system has four equilibria in the boundary of $\mathbb{R}^3_+$, namely $E^0(0,0,0)$, $E^1(K,0,0)$, $E^2_i(\hat{x},\hat{y}_1,\hat{y}_2)$, $\ i = 1,2$, where
$\hat{x} = K\left(1 - \frac{1}{r}\frac{m_i - d_i}{a_i}\right)$, if $\frac{m_i - d_i}{a_i} < r$, $\hat{y}_i = \frac{m_i - d_i}{d_i a_i}\hat{x}$, if $\ m_i > d_i$, $\hat{y}_j = 0$ $i = 1$ or 2, $j = 2$ or 1 and $j \neq i$.

Linearizing (15) in E^1 we get the following interaction matrix:

$$\begin{bmatrix} -r & -m_1 & -m_2 \\ 0 & m_1 - d_1 & 0 \\ 0 & 0 & m_2 - d_2 \end{bmatrix} \tag{16}$$

which is unstable for $m_i > d_i$ and asymptotically stable for $m_i < d_i$. This is natural, because in case of $m_i < d_i$ the necessary condition of the survival of the predator i does not hold ($i = 1, 2$).

Linearizing (15) in E^2_1, ($\hat{y}_1 \neq 0, \ \hat{y}_2 = 0$, analogously the case $\hat{y}_1 = 0, \ \hat{y}_2 \neq 0$) we get the following interaction matrix:

$$\begin{bmatrix} r - \frac{2r\hat{x}}{K} - \frac{m_1 a_1 \hat{y}_1^2}{(a_1\hat{y}_1 + \hat{x})^2} & -\frac{m_1 \hat{x}^2}{(a_1\hat{y}_1 + \hat{x})^2} & -m_2 \\ \frac{a_1 m_1 \hat{y}_1^2}{(a_1\hat{y}_1 + \hat{x})^2} & -\frac{m_1 a_1 \hat{x}\hat{y}_1}{(a_1\hat{y}_1 + \hat{x})^2} & 0 \\ 0 & 0 & m_2 - d_2 \end{bmatrix}. \tag{17}$$

This matrix is unstable for $m_2 > d_2$ and asymptotically stable for $m_2 < d_2$ and $r - \frac{2r\hat{x}}{K} - \frac{m_1 a_1 \hat{y}_1^2}{(a_1\hat{y}_1 + \hat{x})^2} \leq 0$. The meaning of this latter condition will be clear in the following. The condition

$m_2 < d_2$ means that predator 2 cannot survive.

In order to study the stability of E^0 we introduce the variables: $z_i = \dfrac{y_i}{x}$, $i = 1, 2$, that are the quantities of predators respective to a unit quantity of prey. Thus, we can transform the system (15) into the following form:

$$\left.\begin{array}{rcl} \dot{x} & = & x\left(r\left(1-\dfrac{x}{K}\right)-\sum\limits_{j=1}^{2} z_j \dfrac{m_j}{a_j z_j + 1}\right) \\ \dot{z}_i & = & z_i\left(\dfrac{m_i}{a_i z_i + 1} - d_i - r\left(1-\dfrac{x}{K}\right) + \displaystyle\sum_{j=1}^{2} z_j \dfrac{m_j}{a_j z_j + 1}\right), \quad i = 1, 2. \end{array}\right\} \tag{18}$$

This system has no singularity at $(0, 0, 0)$. We can linearize it. We get:

$$\begin{bmatrix} r & 0 & 0 \\ 0 & m_1 - d_1 - r & 0 \\ 0 & 0 & m_2 - d_2 - r \end{bmatrix}. \tag{19}$$

This matrix is unstable for any $r > 0$, independently of $m_i - d_i$.

The most interesting equilibrium point of (15) is the point $E^*(x^*, y_1^*, y_2^*)$ where

$$x^* = K\left(1 - \frac{1}{r}\sum_{i=1}^{2}\frac{m_i - d_i}{a_i}\right), \qquad y_i^* = \frac{m_i - d_i}{d_i a_i} x^*, \tag{20}$$

that represents the coexistence of all the species. We are going to study the stability.

E^* is in the positive octant if

$$\sum_{i=1}^{2}\frac{m_i - d_i}{a_i} < r. \tag{21}$$

$m_i - d_i$ is the maximal growth rate of the predator i. (21) means that the sum of the ratios of the growth rates and half saturation constants of the predators is less than the intrinsic growth rate of the prey. This is natural, because if the growth rate of predators were high it would result in a too fast decreasing of prey, and too low half saturation constants of predators mean that they increase under low quantity of prey relative to predator. Both cases involve the too fast decreasing of prey.

Now the K-, and r-strategist have different roles. In paper [8] a_i was the half saturation constant and it meant the quantity of prey at which the birth rate of predator i was half of its supremum. Now the supremum of the birth rate of the predator i remained m_i. The function p_i tends to its supremum when $\frac{x}{y_i} \to \infty$. But the per capita birth rate is half of the supremum $\left(\frac{\dot{y}_i}{y_i} = \frac{m_i}{2}\right)$, when $\frac{x}{y_i} = a_i$ i.e. a_i means a proportion of prey to predator at which the birth rate is half of its supremum. In the paper cited the predator was called r-strategist whose half saturation constant was greater, the other one was called K-strategist. Now, we maintain the name r-strategist for the predator that has higher half saturation constant. Thus, we call predator 1 the r-strategist and predator 2 the K-strategist when $a_1 > a_2$. At the same time the r-strategist should have a higher birth rate-death rate ratio: $\frac{m_1}{d_1} > \frac{m_2}{d_2}$ (see [9]). However, now the inequality

$$\frac{\frac{m_1}{d_1} - 1}{a_1} > \frac{\frac{m_2}{d_2} - 1}{a_2}$$

should also hold for the advantage of the r-strategist over the K-strategist. This shows that the ratio-dependence has finer properties than older models.

In order to consider the stability of E^* let us linearize (15) in E^*. We get the following interaction matrix:

$$A = \begin{bmatrix} x^*\left(-\frac{r}{K} + \frac{m_1 y_1^*}{(a_1 y_1^* + x^*)^2} + \frac{m_2 y_2^*}{(a_2 y_2^* + x^*)^2}\right) & -\frac{m_1 {x^*}^2}{(a_1 y_1^* + x^*)^2} & -\frac{m_2 {x^*}^2}{(a_2 y_2^* + x^*)^2} \\ \frac{a_1 m_1 {y_1^*}^2}{(a_1 y_1^* + x^*)^2} & -\frac{m_1 a_1 x^* y_1^*}{(a_1 y_1^* + x^*)^2} & 0 \\ \frac{a_2 m_2 {y_2^*}^2}{(a_2 y_2^* + x^*)^2} & 0 & -\frac{m_2 a_2 x^* y_2^*}{(a_2 y_2^* + x^*)^2} \end{bmatrix}. \qquad (22)$$

Theorem 2.1. *(22) is sign-stable and E^* is an asymptotically stable equilibrium point of system*

(15) if

$$\sum_{i=1}^{2} \frac{m_i^2 - d_i^2}{a_i m_i} \leq r. \tag{23}$$

Proof. After a short calculation we get, the entries of the main diagonal of (22) are non-positive under conditions (21), (23). The products of the entries symmetrical to the main diagonal are trivially negative or zero. The graph of (22) is a tree. Both the ε- and the δ-coloring of the graph are trivial, thus, Theorem 2.6 of [15] holds. □

(23) can be written in the following form:

$$\sum_{i=1}^{2} \frac{m_i - d_i}{a_i} \left(1 + \frac{d_i}{m_i}\right) \leq r,$$

thus, it implies (21). Condition (23) means that the prey reproduces well but the predators not as much. Apart from this the parameters may assume arbitrary feasible value. In this case the equilibrium point E^* is asymptotically stable for any K. Of course $x^* < K$ implies a limit for predators too. This is a main difference between the Holling and the ratio-dependent Holling-Menten models. Moreover ratio-dependence may involve structural stability in the positive octant. If we compare the graphs of the systems without and with ratio-dependence, it can be seen that those are the same, but in the first case the zero entries in the main diagonal cause the existence of nontrivial colorings of it, while with ratio-dependence the behavior of the system is simpler, but closer to the reality, because the paradox of enrichment cannot occur (cf. [9]).
We show some trajectories in Figure (1) modeling asymptotic stability of E^*.

Now we enter to study the n-dimensional case.

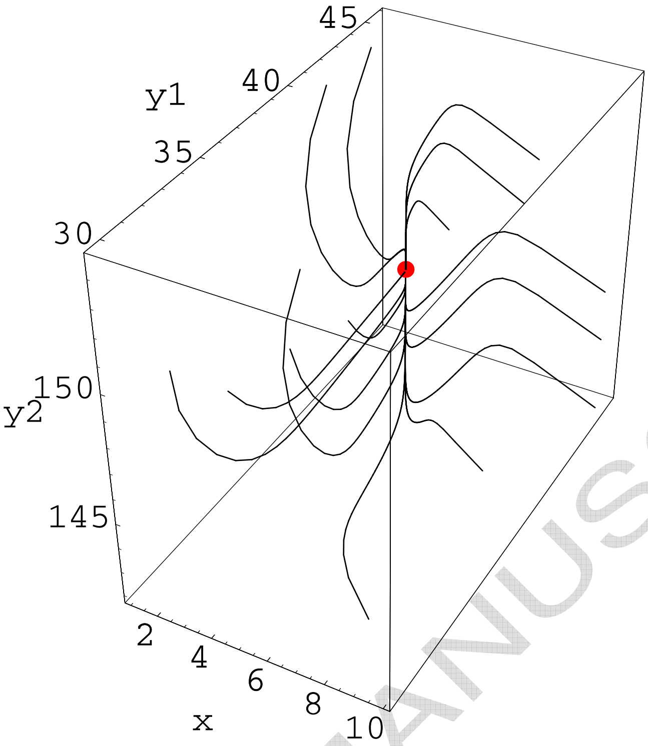

Figure 1: Time evolution of system (15) when (23) holds.

2.2 The n-dimensional case

Let us consider the generalization of system (15) for dimension n:

$$\left.\begin{aligned} \dot{x} &= rx\left(1-\frac{x}{K}\right)-\sum_{i=1}^{n} m_i\frac{xy_i}{a_iy_i+x} \\ \dot{y}_i &= m_i\frac{xy_i}{a_iy_i+x}-d_iy_i, \quad i=1,\ldots,n \end{aligned}\right\}. \tag{24}$$

System (24) can be extended the same way as system (15). The equilibrium points of the extension of (24) on the boundary are $E^0(0,\ldots,0)$, $E^1(K,0,\ldots,0)$, $E_i^2(\hat{x},\hat{y}_1,\ldots,\hat{y}_n)$, where one or more $\hat{y}_i$ is or are equal to zero except at least one. We get easily the following results: The interaction

matrix in E^0 is an unstable diagonal matrix. The interaction matrix in E^1 is an upper diagonal matrix and E^1 is asymptotically stable if $m_i - d_i < 0$ for all i. The interaction matrix in E^2 is such a matrix whose entries at the main diagonal are equal to $m_i - d_i$ if $\hat{y}_i = 0$. If this entries are negative and the entry in the first row and column are all less or equal to zero then this matrix is sign stable. (It can be shown the same way as we will prove the following theorem.)
The most interesting equilibrium point is $E^*(x^*, y_1^*, \dots, y_n^*)$, where

$$x^* = K\left(1 - \frac{1}{r}\sum_{i=1}^{n}\frac{m_i - d_i}{a_i}\right), \quad y_i^* = \frac{m_i - d_i}{d_i a_i}x^*. \tag{25}$$

Let us study the point E^*. It is in the positive orthant if

$$\sum_{i=1}^{n}\frac{m_i - d_i}{a_i} < r. \tag{26}$$

Let us linearize (24) in E^*. We get the following interaction matrix:

$$A = \begin{bmatrix} x^*\left(-\frac{r}{K} + \sum_{i=1}^{n}\frac{m_i y_i^*}{(a_i y_i^* + x^*)^2}\right) & -\frac{m_1 x^{*2}}{(a_1 y_1^* + x^*)^2} & \dots & \dots & -\frac{m_n x^{*2}}{(a_n y_n^* + x^*)^2} \\ \frac{a_1 m_1 y_1^{*2}}{(a_1 y_1^* + x^*)^2} & -\frac{m_1 a_1 x^* y_1^*}{(a_1 y_1^* + x^*)^2} & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{a_n m_n y_n^{*2}}{(a_n y_n^* + x^*)^2} & 0 & \dots & 0 & -\frac{m_n a_n x^* y_n^*}{(a_n y_n^* + x^*)^2} \end{bmatrix}. \tag{27}$$

Theorem 2.2. *(27) is sign-stable and E^* is an asymptotically stable equilibrium point of system (24) if*

$$\sum_{i=1}^{n}\frac{m_i^2 - d_i^2}{a_i m_i} \leq r. \tag{28}$$

Proof. Similar to the the 3-dimensional case, the entries of the main diagonal of (27) are non-positive under conditions (26), (28). The products of the entries symmetrical to the main diagonal are trivially negative or zero. The graph of (27) is a tree. Both the ε- and the δ-coloring of the graph are trivial, thus, the Theorem 2.6 of [15] holds again. □

(28) can be written in the following form:

$$\sum_{i=1}^{n} \frac{m_i - d_i}{a_i} \left(1 + \frac{d_i}{m_i}\right) \leq r,$$

thus, it implies (26), and comments similar to those at the end of Section 2.1 can be made. Our results correspond to Theorem 2.4.2 of [9] because both (15)and (24) are Kolmogorov systems. This means that the situation can be extended to the case of n prey and one predator. We are going to publish it in a following paper.

Now we enter to study the 3-dimensional case of ratio-dependent Ivlev functional response.

3 The Ivlev type functional response

3.1 The 3-dimensional case

Let us consider system (1) in case of (5) and (14). We get:

$$\left.\begin{array}{rcl} \dot{x} & = & rx\left(1 - \frac{x}{K}\right) - m_1 y_1 \left(1 - e^{-\frac{x}{a_1 y_1}}\right) - m_2 y_2 \left(1 - e^{-\frac{x}{a_2 y_2}}\right) \\ \dot{y}_1 & = & m_1 y_1 \left(1 - e^{-\frac{x}{a_1 y_1}}\right) - d_1 y_1 \\ \dot{y}_2 & = & m_2 y_2 \left(1 - e^{-\frac{x}{a_2 y_2}}\right) - d_2 y_2 \end{array}\right\} . \qquad (29)$$

We consider the equilibrium point in the interior of the positive octant only. (In the interior of the positive octant the theorem of existence and uniqueness holds. This region is invariant and the solutions are bounded.) The equilibrium point of the interior of the positive octant is: $E^*(x^*, y_1^*, y_2^*)$, where

$$x^* = K\left(1 - \frac{1}{r}\sum_{i=1}^{2} \frac{d_i}{a_i \ln \frac{m_i}{m_i - d_i}}\right), \quad y_i^* = \frac{1}{a_i \ln \frac{m_i}{m_i - d_i}} x^*. \qquad (30)$$

E^* is in the positive octant if

$$\sum_{i=1}^{2} \frac{d_i}{a_i \ln \frac{m_i}{m_i - d_i}} < r. \tag{31}$$

holds. (The meaning of this condition is similar to the one in case of the Michaelis-Menten model.) Some words on the role of the K-, and r-strategist: The supremum of the birth rate of the predator i is m_i, p_i tends to its supremum when $\frac{x}{y_i} \to \infty$ again. But the per capita birth rate is half of the supremum, when $\frac{x}{y_i \ln 2} = a_i$ and a_i means a proportion of prey to predator again. We will call predator 1 an r-strategist, if its half saturation constant is greater. Thus we call predator 1 an r-strategist, and 2 a K-strategist when $a_1 > a_2$ according to the earlier. But the r-strategist should have its birth rate relative to the death rate higher than the K-strategist, namely $\frac{m_1}{d_1} > \frac{m_2}{d_2}$ should hold. The r-strategist has advantage over the K-strategist only if

$$\frac{1}{a_1 \ln \frac{m_1}{m_1 - d_1}} > \frac{1}{a_2 \ln \frac{m_2}{m_2 - d_2}},$$

namely the birth rate relative to the death rate has to be even greater than the ratio of the half saturation rates. If this does not occur then the r-strategist has no advantage over the K-strategist. The situation is the same as in case of Michaelis-Menten model.

In order to consider the stability of E^* let us linearize (29) in E^*. We get the following interaction matrix:

$$A = \begin{bmatrix} r\left(1 - \frac{2x^*}{K}\right) - \frac{m_1 - d_1}{a_1} - \frac{m_2 - d_2}{a_2} & -d_1 + \frac{x^*}{a_1 y_1^*}(m_1 - d_1) & -d_2 + \frac{x^*}{a_2 y_2^*}(m_2 - d_2) \\ \frac{m_1 - d_1}{a_1} & -(m_1 - d_1) \ln \frac{m_1}{m_1 - d_1} & 0 \\ \frac{m_2 - d_2}{a_2} & 0 & -(m_2 - d_2) \ln \frac{m_2}{m_2 - d_2} \end{bmatrix}. \tag{32}$$

Theorem 3.1. *(32) is sign-stable and E^* is an asymptotically stable equilibrium point of system (29) if*

$$\sum_{i=1}^{2} \frac{2d_i}{a_i \ln \frac{m_i}{m_i-d_i}} - \frac{m_i-d_i}{a_i} \leq r. \tag{33}$$

Proof. A short calculation shows that the entries of the main diagonal of (32) are non-positive under the conditions (31),(33). The products of the entries symmetrical to the main diagonal are negative (or zero) if $-d_i + \frac{x^*}{a_i y_i^*}(m_i - d_i) < 0$ holds. To see this:

$$\frac{x^*}{a_i y_i^*} < \ln \frac{m_i}{m_i-d_i} = \ln\left(1 + \frac{d_i}{m_i-d_i}\right) < \frac{d_i}{m_i-d_i}.$$

The graph of (32) is a tree. Both of the ε- and the δ-coloring of the graph are trivial, thus, Theorem 2.6 of [15] holds. □

Comparing (31) and (33), we get that (33) is stricter. In order to see this, we show, that $\frac{d_i}{\ln \frac{m_i}{m_i-d_i}} > m_i - d_i$. Rearranging the trivially true inequality $\ln \frac{m_i}{m_i-d_i} < \frac{m_i}{m_i-d_i} - 1$ the previous statement follows.

(33) means that if the the prey reproduces well but the predators not as much then the equilibrium point E^* is asymptotically stable for any K. Of course $x^* < K$. This is a main difference between the Ivlev and the ratio-dependent Ivlev models. Moreover ratio-dependence may involve the structural stability. If we compare the graphs of the system with and without ratio-dependence, it can be seen again that those are the same, but in the latter case the zero entries in the main diagonal cause the existence of trivial colorings of it, while with ratio-dependence the behavior of the system is simpler, but perhaps closer to the reality, because the paradox of enrichment cannot occur (cf. [16]).

We show some trajectories in Figure 2 modeling asymptotic stability of E^*.

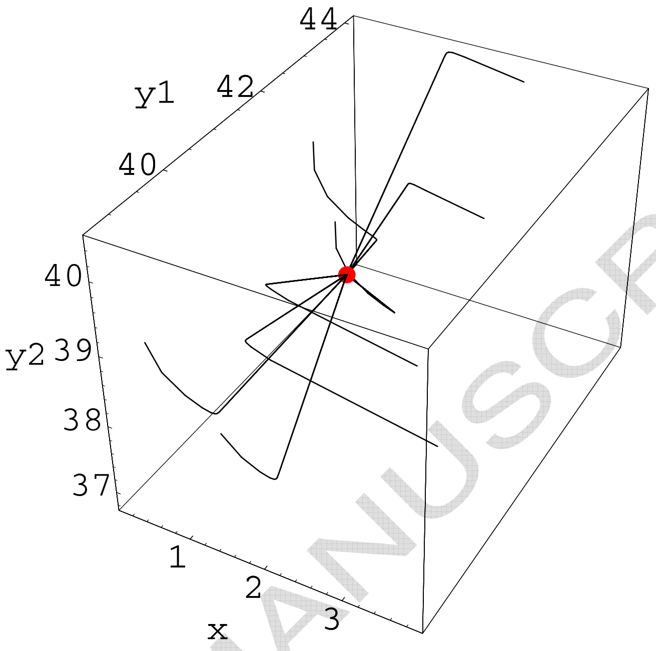

Figure 2: Time evolution of system (29) when (33) holds.

Now we turn to the study of the n-dimensional case of the ratio-dependent Ivlev model. We state our results briefly, because those are direct generalizations of this Section.

3.2 The n-dimensional case

Let us consider generalization of system (29) for dimension n:

$$\left.\begin{array}{rcl} \dot{x} & = & rx\left(1-\frac{x}{K}\right)-\sum\limits_{i=1}^{n} m_i y_i\left(1-e^{-\frac{x}{a_i y_i}}\right) \\ \dot{y}_i & = & m_i y_i\left(1-e^{-\frac{x}{a_i y_i}}\right)-d_i y_i, \quad i=1,\ldots,n \end{array}\right\}. \qquad (34)$$

We consider the equilibrium point in the interior of the positive orthant only that is $E^*(x^*, y_1^*, \ldots, y_n^*)$, where

$$x^* = K\left(1 - \frac{1}{r}\sum_{i=1}^{n}\frac{d_i}{a_i \ln\frac{m_i}{m_i - d_i}}\right), \quad y_i^* = \frac{1}{a_i \ln\frac{m_i}{m_i - d_i}} x^*. \tag{35}$$

E^* is in the positive orthant if

$$\sum_{i=1}^{n}\frac{d_i}{a_i \ln\frac{m_i}{m_i - d_i}} < r. \tag{36}$$

Let us linearize (34) in E^*. We get the following interaction matrix:

$$A = \begin{bmatrix} r\left(1 - \frac{2x^*}{K}\right) - \sum_{i=1}^{n}\frac{m_i - d_i}{a_i} & -d_1 + \frac{x^*}{a_1 y_1^*}(m_1 - d_1) & \ldots & \ldots & -d_n + \frac{x^*}{a_n y_n^*}(m_n - d_n) \\ \frac{m_1 - d_1}{a_1} & -(m_1 - d_1)\ln\frac{m_1}{m_1 - d_1} & 0 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{m_n - d_n}{a_n} & 0 & \ldots & 0 & -(m_n - d_n)\ln\frac{m_n}{m_n - d_n} \end{bmatrix}. \tag{37}$$

Theorem 3.2. *(37) is sign-stable and E^* is an asymptotically stable equilibrium point of system (34) if*

$$\sum_{i=1}^{n}\frac{2d_i}{a_i \ln\frac{m_i}{m_i - d_i}} - \frac{m_i - d_i}{a_i} \leq r. \tag{38}$$

Proof. Similar to the the 3-dimensional case, the conditions of Theorem 2.6 of [15] hold again. ☐

In order to show that (34) is a Kolmogorov system one has to expand the righthand side of the first equation into power series. Thus Theorem 2.4.2. of [9] is not easy to use while our theorem is applicable. Condition (38) is stricter than (36). The meaning of the condition (38) is the same as it was in case of the Michaelis-Menten model. Thus, we can generalize the whole problem.

4 The n-dimensional general model

Let us consider system (1) with the most general ratio-dependent functional response: $p_i(x, y_i, a_i) := p_i\left(\frac{y_i}{x}\right)$ (to save space we do not write out the dependence on a_i):

$$\left.\begin{array}{rcl} \dot{x} & = & rxg(x,K) - \displaystyle\sum_{i=1}^{n} y_i p_i\left(\frac{y_i}{x}\right) \\ \dot{y}_i & = & y_i p_i\left(\frac{y_i}{x}\right) - d_i y_i, \quad i = 1, 2, \ldots, n \end{array}\right\}. \tag{39}$$

This model was studied without ratio-dependence by Ferreira in [13] where a Zip-bifurcation was proved.

We consider this system in the interior of the positive orthant. Suppose that there exists an equilibrium point $E^*(x^*, y_1^*, \ldots, y_n^*)$ in the positive orthant, where x^*, and y_i^* are the solutions of the following equations:

$$rxg(x,K) = \sum_{i=1}^{n} d_i y_i, \quad p_i\left(\frac{y_i}{x}\right) = d_i, \quad i = 1, \ldots, n. \tag{40}$$

It is easy to see, that $x^* > 0$ iff $K > x^*$ but this is natural since equilibria cannot exist above the carrying capacity of the environment. The coefficient matrix of (39) in E^* denoted by A is:

$$\begin{bmatrix} a_{11} & -d_1 - y_1^* p_1'\left(\frac{y_1^*}{x^*}\right)\frac{1}{x^*} & \ldots & \ldots & -d_n - y_n^* p_n'\left(\frac{y_n^*}{x^*}\right)\frac{1}{x^*} \\ y_1^* p_1'\left(\frac{y_1^*}{x^*}\right)\left(-\frac{y_1^*}{x^{*2}}\right) & y_1^* p_1'\left(\frac{y_1^*}{x^*}\right)\frac{1}{x^*} & 0 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ y_n^* p_n'\left(\frac{y_n^*}{x^*}\right)\left(-\frac{y_n^*}{x^{*2}}\right) & 0 & \ldots & 0 & y_n^* p_n'\left(\frac{y_n^*}{x^*}\right)\frac{1}{x^*} \end{bmatrix} \tag{41}$$

where

$$a_{11} = rg(x^*,K) + rx^* g_x'(x^*,K) - \sum_{i=1}^{n} y_i^* p_i'\left(\frac{y_i^*}{x^*}\right)\left(-\frac{y_i^*}{x^{*2}}\right), \tag{42}$$

and $p_i'\left(\frac{y_i}{x}\right) = \dfrac{dp_i\left(\frac{y_i}{x}\right)}{d\left(\frac{y_i}{x}\right)}$.

Theorem 4.1. *(41) is sign-stable and E^* is an asymptotically stable equilibrium point of system (39) if*

$$a_{11} \leq 0, \tag{43}$$

$$p_i'\left(\frac{y_i^*}{x^*}\right) < 0, \quad i = 1, \dots, n, \tag{44}$$

and

$$-d_i - y_i^* p_i'\left(\frac{y_i^*}{x^*}\right)\frac{1}{x^*} < 0, \quad i = 1, \dots, n. \tag{45}$$

Proof. As it was done earlier one has to control whether the conditions of Theorem 2.6 of [15] hold.

The entry $a_{11} \leq 0$ by (43), while the other entries in the main diagonal are negative because of (44). The products of the entries symmetrical to the main diagonal are negative or zero because of (44), (45). The graph of this matrix is a tree rooted in vertex 1, which is white if $a_{11} = 0$, thus the graph has not got any cycles. Both of the colorings ε and δ have to satisfy the condition that black vertex has not got a single white neighbour. All vertices are black, at most except of one because of (44) is strict. Thus, every black vertex can have only one white neighbour, this is vertex 1. Hence the vertex 1 has to be black. We get that all ε- and δ-colorings are trivial, all conditions of Theorem 2.6 of [15] hold and A is sign-stable. $\square$

In order to understand the meaning of condition (44) let us consider the following derivative: $\left(\frac{\dot{y}_i}{y_i}\right)'_{y_i} = p_i'\left(\frac{y_i}{x}\right)\frac{1}{x} < 0$, $i = 1, \dots, n$. All of these inequalities are strict which means that there is intraspecific competition within all predator species. If $x > 0$, (44) means, there is intraspecific competition in all predator species. The condition (45) means y_i is predator of x, i.e. $\left(\frac{\dot{x}}{x}\right)'_{y_i} = \frac{1}{x}\left(-p_i\left(\frac{y_i}{x}\right) - y_i p_i'\left(\frac{y_i}{x}\right)\frac{1}{x}\right) < 0$ and this also holds at E^*, where $p_i(\frac{y_i^*}{x^*}) = d_i$. Comparing matrix (41) with the matrix given in the third section of [13] we can see that in Ferreira's paper all entries in the main diagonal in (44) could be zero, and this involves the occuring of the zip-bifurcation. In our system the zip-bifurcation cannot occur. The coexistence of the species does not depend on K. But E^* exists iff $x^* < K$ thus x^* has an upper limit depending on K. The parameter r is the intrinsic growth rate of prey which obviously cannot be arbitrary high. The prey species determines it. The sum of the quantity of the predators is an increasing function of x^* (in case of $x^* < K$). Clearly, more predator need more food. Under conditions (43)-(45) all the predator species can coexist with the prey, whose maximal number has a limit K. The exact quantity of the different species is determined by the specific values of the parameters. Under these conditions the model may be structurally stable as opposed to the model without considering ratio-dependence.

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