

# Technical Notes and Correspondence

## Some Optimization Models of Growth in Biology

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**Abstract**—The presented models are applications of classical optimal control methods in biology. The growth of plants and animals are described by nonlinear ordinary differential equations. Biologically justified limitations provide additional inequality constraints on the control functions and the state variable. The solutions of the optimization models are control functions which either maximize the amounts of energy allocated to reproduction or minimize the age of achieving adult body size.

### I. INTRODUCTION

More than 100 years old and still central in biology is the concept of natural selection. Darwin formulated it as survival of the fittest, i.e., of individuals with features that allow them to leave the largest average number of offspring. This means that natural selection maximizes fitness. It follows from the theory of natural selection that organisms should be well adapted to their environmental conditions. The usefulness of the term “adaptation” has been criticized, however, because this term is not well defined and often leads to circular reasoning. In optimization models we ask for the optimal level of a given feature under a well-defined mathematical model and quantity criterion (fitness). Traditionally, biologists have formulated the theory of natural selection in words, without mathematical notation. Although the first serious mathematical models were introduced into evolutionary theory in the 1920's, control theory methods were applied no earlier than 20 years ago. The application of dynamic optimization based on the Pontryagin maximum principle is even more recent. The results presented in this paper have been published in several biology journals, with the emphasis of biological aspects. The aim of this paper is to present concisely some nontechnical applications of dynamic optimization.

### II. STATE EQUATIONS

The sizes of an individual's body parts at age  $t$  are described by the positive function  $x(t) \in \mathbf{R}^n$ , which is measured in energy units such as calories. Each element of vector  $x$  is the size of a separate part of the body. Very frequently the first  $n - 1$  elements described the sizes of the vegetative parts of the body, and the last one  $x_n$  is the size of the generative part. The surplus energy acquired by an organism, i.e., energy not used for maintenance, is denoted by the scalar positive function  $f(x)$ . This energy flux is allocated between vegetative and generative growth. It follows from biological assumptions that  $f: \mathbf{R}^n \rightarrow \mathbf{R}$  is a concave and increasing function. Vector control function  $u(t) \in \mathbf{R}^n$  indicates the fraction of surplus energy going to the growth of  $n$  individual body parts at age  $t$ . Thus

the admissible set of the control function is defined

$$U_a = \left\{ u: u = (u_1, \dots, u_n)^T, u_i \in L^2(0, T), u_i(t) \geq 0, \sum_{i=1}^n u_i(t) = 1 \forall t \in [0, T] \right\} \quad (1)$$

where  $T$  denotes the life span or season length for annual organisms. Negative allocations are impossible; this makes all components of the control positive or equal to zero. It is also assumed that all surplus energy is allocated in an organism which consists of  $n$  subsystems.

Under the above assumptions, the growth of a body is given by the vector ordinary differential equation

$$\dot{x} = uf(x). \quad (2)$$

It is frequently assumed that there are only two equations

$$\begin{cases} \dot{x}_1 = (1 - u)f(x_1) \\ \dot{x}_2 = uf(x_1) \end{cases} \quad 0 \leq u(t) \leq 1 \quad (3)$$

where  $x_1$  represents the vegetative and  $x_2$  the generative part of the body. Scalar control function  $u(t)$  is the fraction of surplus energy that goes to the reproductive part at age  $t$ . The energy flux takes usually the form

$$f(x_1) = \alpha x_1^a - \beta x_1^b \quad (4)$$

where constant coefficients fulfil inequalities:  $0 < a \leq b < 1$  and  $0 < \beta < \alpha$ .

Iwasa and Roughgarden [2] presented an example of model (2) for plants. Their model consists of three equations. State equation (3) with linear function  $f(x_1)$  was considered by Vincent and Pulliam [10] and King and Roughgarden [5] as a continuous version of Cohen's problem [1]. The state equations used by Mirmirani and Oster [8] have the form

$$\begin{cases} \dot{x}_1 = \tau x_1 - \mu x_1 & x_1(0) > 0 \\ \dot{x}_2 = (1 - u)\tau x_1 - \nu x_2 & x_2(0) = 0 \end{cases} \quad (5)$$

where coefficients  $\tau, \mu, \nu$  are constant. Terms  $\mu x_1$  and  $\nu x_2$  represent losses of vegetative and reproductive parts. King and Roughgarden [3] used (5) with coefficients depending on time  $t$ . Schaffer *et al.* [9] also considered nonstationary linear state equations that consisted of three equations and three control functions. The additional state equation represented the flux of energy to storage (bulbs, rhizomes, etc.).

### III. QUANTITY CRITERIA

The optimization problem consists of finding the vector function  $u \in U_a$  which satisfies assumptions (1) and (2) and maximizes the functional

$$Q = x_n(T). \quad (6)$$

In biological interpretation optimal allocation of energy maximizes fitness defined by (6). This criterion, which is equivalent to the expected number of offspring, was adopted in [1]–[3] and [7]–[11]. Such a fitness measure is justified for annual organisms as well as for stationary populations.

The nesting period is the most dangerous in a bird's life, because of extremely high predator pressure. This means that natural selection

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should minimize the time spent in the nest. Thus we can expect optimal resource allocation to the alimentary tract (the engine that drives growth) and the rest of the body. This case, considered by Konarzewski *et al.* [6], exemplifies the minimum time problem. The optimal solution is a time-dependent fraction of energy going into the growth of the digestive tract in such a way that the development period  $T$  is reduced to a minimum.

#### IV. INEQUALITY CONSTRAINTS

The inequality constraint for state variables was considered by Konarzewski *et al.* [6]. It was assumed that the maximum ratio of alimentary tract weight  $x_1$  to body weight  $x_1 + x_2$  for nestling birds cannot exceed a constant  $c < 1$

$$\frac{x_1}{x_1 + x_2} \leq c. \quad (7)$$

Kozłowski and Ziólko [7] considered the biologically justified assumption that the reproductive growth rate is limited by the current size of the reproductive organ. This leads to the differential inequality constraint

$$\dot{x}_n \leq g(x_n) \quad (8)$$

where  $g$  is an increasing and  $C^1$  continuous function.

#### V. OPTIMAL SOLUTION

The dynamic allocation problem is to choose the control  $u(t)$  that maximizes fitness subject to the state equations and inequality constraints. The solutions of optimization problems (1), (2), and (6) were obtained by the Pontryagin maximum principle. The Hamiltonian is usually a linear function of control  $u$ . As the result the optimal solutions have bang-bang forms. Continuous solution  $u(t)$  was obtained for random season length [4]. Kozłowski and Ziólko [7] obtained a gradual switch from growth to reproduction under inequality constraint (8). The solution of the minimum-time problem of allocation of resources in growing nestlings [6], having a bang-bang form, is as follows: all surplus energy should be allocated to the digestive tract to get the maximum allowable proportion (7); then this proportion should be maintained until the final size of the digestive tract  $x_2(T)$  is reached; finally, all surplus energy should be allocated to the rest of the body  $x_1$ .

All the presented optimization problems have unique solutions, although this is not proved in the cited papers. These solutions are globally optimal what makes it easy to compute numerically the optimal solutions from the necessary conditions of optimality.

#### VI. EXAMPLE: NONLINEAR DYNAMIC OPTIMIZATION WITH AN INEQUALITY CONSTRAINT

Surplus energy is partitioned between the vegetative part  $x_1$  and the reproductive part  $x_2$ . The growth of these two subsystems is described by a set of two nonlinear ordinary differential equations

$$\dot{x}_1 = (1 - u)f(x_1) \quad (9)$$

$$\dot{x}_2 = uf(x_1) \quad (10)$$

where  $f$  is the rate at which surplus energy is gained. The initial state, i.e., the sizes of both parts of the body of a given individual at the beginning of the season, is known

$$x_1(0) = x_{10} > 0 \quad (11)$$

$$x_2(0) = x_{20} > 0. \quad (12)$$

The control function

$$0 \leq u(t) \leq 1 \quad u \in L^2(0, T) \quad (13)$$

indicates the fraction of energy going to the reproductive part at age  $t$ . Season length  $T$  is assumed to be constant.

The reproductive subsystem is initially very small, and it may be incapable of absorbing all surplus energy produced by the whole organism. This leads to the inequality constraint

$$\dot{x}_2 \leq g(x_2) \quad (14)$$

where  $g$  is a continuous increasing function (which usually does not differ much from a linear function) of the second state variable (reproductive part). Taking into account state equation (10), inequality constraints (13) and (14) can be written in the form

$$0 \leq u(t) \leq \min\{1, g(x_2(t))/f(x_1(t))\}. \quad (15)$$

The quantity criterion (fitness)

$$Q = x_2(T) - x_2(0) \quad (16)$$

is the difference between the size of reproductive part  $x_2(T)$  at the end of the season and its initial size  $x_2(0)$ . For plants it is the difference between seed yield and the size of the primordium of that part at the beginning of the season.

The optimization problem consists of finding the control function  $u$  which fulfils the inequality constraints (15) and maximizes the functional (16) in terms of state equations (9) and (10) and the initial conditions (11) and (12). For the considered problem the Hamiltonian has the form

$$H = [u(p_2 - p_1) + p_1]f(x_1) \quad (17)$$

where  $p_1$  and  $p_2$  are the solutions of the adjoint equations

$$\dot{p}_1 = -[u(p_2 - p_1) + p_1]f'(x_1) \quad (18)$$

$$\dot{p}_2 = 0 \quad (19)$$

with the final conditions

$$p_1(T) = 0 \quad (20)$$

$$p_2(T) = 1 \quad (21)$$

and  $f'(x_1)$  being the derivative of function  $f$  with respect to  $x_1$ . Equation (19) with final condition (21) has solution

$$p_2(t) = 1. \quad (22)$$

The optimal solution which maximizes Hamiltonian (17) has the form

$$u = \begin{cases} 0 & \text{if } p_1 > 1 \\ g(x_2)/f(x_1) & \text{if } p_1 < 1 \text{ and } f(x_1) > g(x_2) \\ 1 & \text{if } p_1 < 1 \text{ and } f(x_1) \leq g(x_2). \end{cases} \quad (23)$$

Let us now analyze these three cases:

- 1) For control function  $u = 0$  the state equations (9) and (10) obtain the form

$$\dot{x}_1 = f(x_1) \quad (24)$$

$$\dot{x}_2 = 0. \quad (25)$$

Equation (25) with initial condition (12) has solution

$$x_2(t) = x_{20}. \quad (26)$$

The adjoint equation (18) has the form

$$\dot{p}_1 = -p_1 f'(x_1) \quad (27)$$

and solution

$$p_1(t) = \frac{c_1}{f(x_1(t))} \quad (28)$$

where  $c_1$  is a constant depending on the boundary condition.

2) If  $u = g(x_2)/f(x_1)$  then the state equations obtain the form

$$\dot{x}_1 = f(x_1) - g(x_2) \quad (29)$$

$$\dot{x}_2 = g(x_2) \quad (30)$$

and the adjoint equation (18) has solution

$$p_1(t) = \frac{1}{f(x_1(t))} \left[ c_2 - \int_{T_1}^t g(x_2(t))f'(x_1(t))dt \right] \quad (31)$$

where  $c_2$  is a constant and  $T_1$  is the assumed time of beginning of integration.

3) If  $u = 1$  it is easy to find the solution for state and adjoint equations. The state equations have the form

$$\dot{x}_1 = 0 \quad (32)$$

$$\dot{x}_2 = f(x_2) \quad (33)$$

and solutions

$$x_1(t) = c_3 \quad (34)$$

$$x_2(t) = c_4 + f(c_3)(t - T_2). \quad (35)$$

The adjoint equation

$$\dot{p}_1 = -f'(c_3) \quad (36)$$

has solution

$$p_1(t) = c_5 - f'(c_3)(t - T_3) \quad (37)$$

where  $c_3, c_4, c_5, T_2, T_3$  are constants.

For the first case, (27) with condition (20) has solution (28) equal to zero, i.e.,  $c_1 = 0$ . This is contradictory to the Pontryagin maximum principle (23). For the second case, (31) with condition (20) has the form

$$p_1(t) = \frac{1}{f(x_1(t))} \int_t^T g(x_2(t))f'(x_1(t))dt \quad (38)$$

and for the last case, ( $u = 1$ ) (37) with condition (20) reads

$$p_1(t) = f'(c_3)(T - t). \quad (39)$$

Both functions (38) and (39) are equal to zero for  $t = T$  and are positive for sufficiently large  $t < T$ . Thus, there exists a period of time which includes the endpoint, where conditions (23) are satisfied. Continuing the considerations for decreasing time (i.e., from final time  $T$  backward to initial time zero), we obtain five possibilities for an optimal solution.

Case 1:

$$u(t) = g(x_2(t))/f(x_1(t)) \quad \text{for } t \in [0, T]. \quad (40)$$

For this case we obtain from (23) and (38) the characteristic inequality

$$\int_0^T g(x_2(t))f'(x_1(t))dt < f(x_{10}). \quad (41)$$

Case 2:

$$u(t) = 1 \quad \text{for } t \in [0, T]. \quad (42)$$

From (23) and (39) we conclude the inequality

$$f'(x_{10})T < 1. \quad (43)$$

Case 3:

$$u(t) = \begin{cases} 0 & \text{if } 0 \leq t < T_s \\ 1 & \text{if } T_s < t \leq T \end{cases} \quad (44)$$

where  $T_s$  denotes the switching point which fulfils condition

$$f'(x_1(T_s))(T - T_s) = 1. \quad (45)$$

Constraint (14) is inactive. This means that

$$f(x_1(T_s)) \leq g(x_{20}). \quad (46)$$

Case 4:

$$u(t) = \begin{cases} g(x_2(t))/f(x_1(t)) & \text{if } 0 \leq t < T_s \\ 1 & \text{if } T_s < t \leq T \end{cases} \quad (47)$$

For this case we obtain from (23), (31), and (39) the inequality

$$f'(x_1(T_s))f(x_1(T_s))(T - T_s) + \int_0^{T_s} g(x_2(t))f'(x_1(t))dt < f(x_{10}). \quad (48)$$

Moreover, constraint (14) is active until time  $T_s$ , at which

$$f(x_1(T_s)) = g(x_2(T_s)). \quad (49)$$

Case 5:

$$u(t) = \begin{cases} 0 & \text{if } 0 \leq t < T_1 \\ g(x_2(t))/f(x_1(t)) & \text{if } T_1 < t < T_2 \\ 1 & \text{if } T_2 < t \leq T. \end{cases} \quad (50)$$

From (23), (31), and (39) we find that the following equality must hold

$$f(x_1(T_1)) = f(x_1(T_2))f'(x_1(T_2))(T - T_2) + \int_{T_1}^{T_2} g(x_2(t))f'(x_1(t))dt. \quad (51)$$

Constraint (14) is active from time  $T_1$  until time  $T_2$ . This means that

$$f(x_1(T_2)) = g(x_2(T_2)). \quad (52)$$

Although there are five qualitatively different solutions, only the fifth one has biological meaning. The other solutions require biologically unreasonable assumptions, e.g., an enormous initial size of reproductive organs (Case 3); excessively large initial body size (Cases 2 and 4), causing in the extreme event no growth during life (Case 2); or lifetime absorption of more energy than can be used for reproductive production (Case 1). The optimal strategy (50) divides the life span into three parts: pure vegetative growth  $u(t) = 0$ , mixed vegetative and generative growth with  $u(t) = g(x_2(t))/f(x_1(t))$ , and finally pure generative growth  $u(t) = 1$ . The value of the control function in the period of mixed growth results from the maximization of reproductive growth under the active constraint (14). The shapes of functions  $g(x_2)$  and  $f(x_1)$  have a great influence on the switching times  $T_1$  and  $T_2$ . It is biologically justified that  $g(x_2(T_1)) < f(x_1(T_1))$ . Both of these are increasing functions, but  $g(x_2)$  is almost linear and  $f(x_1)$  is concave. This means that there is a switching time  $T_2$  such that  $g(x_2(T_2)) = f(x_1(T_2))$ .

## VII. EXAMPLE: TIME-OPTIMAL PROBLEM

Let us consider the growth of an altricial chick described by a set of differential equations

$$\dot{x}_1 = u f(x_1, x_2) \quad (53)$$

$$\dot{x}_2 = (1 - u)f(x_1, x_2) \quad (54)$$

where control function  $u$  is the fraction of energy allocated to growth of the digestive tract  $x_1$ . The second variable  $x_2$  is the weight of the rest of body. The control function satisfies conditions

$$0 \leq u(t) \leq 1 \quad u \in L^2(0, T) \quad (55)$$

where the initial time is the chick's hatching and  $T$  is the final time, i.e., the age at fledging. The flux of surplus energy  $f(x_1, x_2)$  is a  $C^1$  continuous function which satisfies inequality constraints

$$f(x_1, x_2) > 0 \quad (56)$$

$$\partial f(x_1, x_2)/\partial x_1 > 0 \quad (57)$$

$$\partial f(x_1, x_2)/\partial x_2 < 0 \quad (58)$$

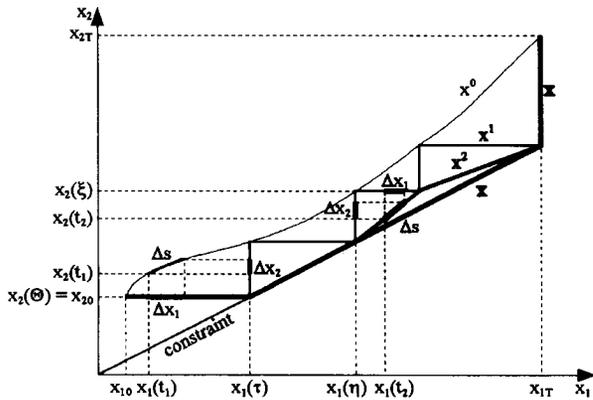


Fig. 1. The sequence of trajectories convergent to the optimal trajectory  $x$  for the arbitrary admissible trajectory  $x^0$ .

for every  $x_1 > 0$  and  $x_2 > 0$ . This means that the flux of surplus energy is an increasing function of the size of the digestive tract. On the other hand, the cost of maintenance is higher for a large organism. This makes the flux of surplus energy a decreasing function of the size of the rest of the body.

The initial state at hatching and the final state at fledging are known and satisfy conditions

$$\begin{aligned} 0 < x_1(0) = x_{10} < x_1(T) = x_{1T} \\ 0 < x_2(0) = x_{20} < x_2(T) = x_{2T}. \end{aligned} \quad (59)$$

Throughout all of a chick's development, the maximum ratio of alimentary tract size to body size cannot exceed a positive constant  $c < 1$

$$\frac{x_1}{x_1 + x_2} \leq c. \quad (60)$$

The optimization problem consists of finding the control function  $u$  which satisfies the constraints (55) and which in terms of state equations (53) and (54) and inequality (60) leads the system from the initial state to the final state in the minimal time. The solution describes the optimal allocation of energy between the development of the alimentary tract (the engine supplying energy) and the rest of the body. Natural selection should prefer such a strategy in altricial birds.

Here we sketch out a proof that, under additional assumptions (56)–(58), the solution (see Fig. 1) of the considered optimization problem has the form

$$u(t) = \begin{cases} 1 & \text{if } \frac{x_1(t)}{x_1(t)+x_2(t)} < c \text{ and } x_1(t) < x_{1T} \\ c & \text{if } \frac{x_1(t)}{x_1(t)+x_2(t)} = c \text{ and } x_1(t) < x_{1T} \\ 0 & \text{if } x_1(t) = x_{1T} \text{ and } x_2(t) < x_{2T}. \end{cases} \quad (61)$$

The set of admissible states (see Fig. 1) is bounded by the  $x_2$ -axis and by the line  $x_2 = (1 - c)x_1/c$ . The state variables are positive and nondecreasing functions of time  $t$ . To prove that the control defined by (61) is time optimal, we shall show that for every other admissible control  $u^0$  in  $L^2$  for which the respective trajectory  $x^0$  satisfies boundary conditions (59) it is possible to construct a sequence of admissible controls  $u^i$  ( $i = 0, 1, 2, \dots$ ) such that  $u^i$  is better than  $u^j$  if  $i > j$ . The trajectories  $x^i$  ( $i = 0, 1, 2, \dots$ ) reach the final condition at time  $T_i$ . It follows from the construction that the sequence  $T_i$  strictly decreases and is convergent to optimal  $T$ . Fig. 1 presents the method for construction of such a sequence.

The time required to pass the segment of trajectory  $\Delta s$  (see the left part of Fig. 1) is given by the formula

$$\Delta t = \frac{\Delta s}{f(x_1(t_1), x_2(t_1))\sqrt{u^2(t_1) + (1 - u(t_1))^2}} + o(\Delta s) \quad (62)$$

where  $o(\Delta s)$  is a small residuum of an order greater than one with respect to  $\Delta s$ . The time required to pass the segments parallel to the axes is given by the formulas

$$\Delta t_1 = \frac{\Delta x_1}{f(x_1(t_1), x_2(\theta))} + o(\Delta x_1) \quad (63)$$

$$\Delta t_2 = \frac{\Delta x_2}{f(x_1(\tau), x_2(t_1))} + o(\Delta x_2). \quad (64)$$

For a sufficiently small  $\Delta s$  we obtain the inequality

$$\begin{aligned} \Delta t_1 + \Delta t_2 &\leq \frac{\Delta x_1 + \Delta x_2}{\tilde{f}} \\ &= \frac{\Delta s(\cos(\varphi) + \sin(\varphi))}{\tilde{f}} + o(\Delta s) \end{aligned} \quad (65)$$

where

$$\tilde{f} = \min\{f(x_1(t_1), x_2(\theta)), f(x_1(\tau), x_2(t_1))\} \quad (66)$$

and

$$\begin{aligned} \Delta x_1 &= \Delta s \cos(\varphi) + o(\Delta s) \\ \Delta x_2 &= \Delta s \sin(\varphi) + o(\Delta s). \end{aligned} \quad (67)$$

Taking into account that

$$\sin(\varphi) + \cos(\varphi) = \frac{1}{\sqrt{u^2(t_1) + (1 - u(t_1))^2}} \quad (68)$$

we obtain from the inequality (65)

$$\Delta t_1 + \Delta t_2 - \Delta t \leq F(t_1) \frac{\Delta s}{\sqrt{u^2(t_1) + (1 - u(t_1))^2}} + o(\Delta s) \quad (69)$$

where

$$F(t_1) = \left( \frac{1}{\tilde{f}} - \frac{1}{f(x_1(t_1), x_2(t_1))} \right) \leq 0 \quad (70)$$

because

$$\tilde{f} \geq f(x_1(t_1), x_2(t_1)) \quad (71)$$

results from definition (66) and the assumed inequalities (57) and (58). From inequality (69) we conclude that the trajectory  $x^1$  (see Fig. 1) needs less time to pass than the arbitrarily taken trajectory  $x^0$ .

In a similar way we proceed to prove that the third trajectory  $x^2$  in Fig. 1) is better than trajectory  $x^1$ . For this case (presented on the right side of Fig. 1) let us first notice that

$$\Delta t = \frac{\Delta s}{f(x_1(t_2), x_2(t_2))\sqrt{u^2(t_2) + (1 - u(t_2))^2}} + o(\Delta s) \quad (72)$$

and

$$\Delta t_1 = \frac{\Delta x_1}{f(x_1(t_2), x_2(\xi))} + o(\Delta x_1) \quad (73)$$

$$\Delta t_2 = \frac{\Delta x_2}{f(x_1(\eta), x_2(t_2))} + o(\Delta x_2). \quad (74)$$

For a sufficiently small  $\Delta s$  we obtain

$$\Delta t_1 + \Delta t_2 \geq \frac{\Delta x_1 + \Delta x_2}{\tilde{f}} = \frac{\Delta s(\cos(\psi) + \sin(\psi))}{\tilde{f}} \quad (75)$$

where

$$\tilde{f} = \max\{f(x_1(t_2), x_2(\xi)), f(x_1(\eta), x_2(t_2))\} \quad (76)$$

and

$$\begin{aligned} \Delta x_1 &= \Delta s \cos(\psi) \\ \Delta x_2 &= \Delta s \sin(\psi). \end{aligned} \quad (77)$$

Taking into account that

$$\sin(\psi) + \cos(\psi) = \frac{1}{\sqrt{u^2(t_2) + (1-u(t_2))^2}} \quad (78)$$

we finally obtain from inequality (75)

$$\Delta t_1 + \Delta t_2 - \Delta t \geq F(t_2) \frac{\Delta s}{\sqrt{u^2(t_2) + (1-u(t_2))^2}} + o(\Delta s) \quad (79)$$

where

$$F(t_2) = \left( \frac{1}{\bar{f}} - \frac{1}{f(x_1(t_2), x_2(t_2))} \right) \geq 0 \quad (80)$$

results from definition (76) and assumptions (57) and (58). In a similar way we can construct other "better" trajectories which converge to the optimal trajectory  $x$  (see Fig. 1) defined by control (61).

Field data show that in altricial birds, the ratio of the initial size of the digestive tract to the body size is equal to  $c$  at hatching. Natural selection in embryonic development, not considered in the model, should lead to such a ratio. During the first part of postembryonic development, surplus energy should be allocated to the digestive tract at the highest rate permitted by inequality (60). At a certain time the alimentary tract reaches its final size and then all energy is allocated to the rest of the body.

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#### REFERENCES

- [1] D. Cohen, "Maximizing final yield when growth is limited by time or by limiting resources," *J. Theor. Biol.*, vol. 33, pp. 299-307, 1971.
- [2] Y. Iwasa and J. Roughgarden, "Shoot/root balance of plants: Optimal growth of a system with many vegetative organs," *Theor. Pop. Biol.*, vol. 25, pp. 78-105, 1984.
- [3] D. King and J. Roughgarden, "Multiple switches between vegetative and reproductive growth in annual plants," *Theor. Pop. Biol.*, vol. 21, pp. 194-204, 1982.
- [4] —, "Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length," *Theor. Pop. Biol.*, vol. 22, pp. 1-16, 1982.
- [5] —, "Energy allocation patterns of the California grassland annuals *Plantago erecta* and *Clarkia rubicunda*," *Ecology*, vol. 64, pp. 16-24, 1983.
- [6] M. Konarzewski, J. Kozłowski, and M. Ziólko, "Optimal allocation of energy to growth of the alimentary tract in birds," *Func. Ecol.*, vol. 3, pp. 589-596, 1989.
- [7] J. Kozłowski and M. Ziólko, "Gradual transition from vegetative to reproductive growth is optimal when the maximum rate of reproductive growth is limited," *Theor. Pop. Biol.*, vol. 34, pp. 118-129, 1988.
- [8] M. Mirmirani and G. Oster, "Competition, kin selection, and evolutionary stable strategy," *Theor. Pop. Biol.*, vol. 13, pp. 304-339, 1978.
- [9] W. M. Schaffer, R. S. Inouye, and T. S. Whittam, "Energy allocation by an annual plant when the effect of seasonality on growth and reproduction are decoupled," *Amer. Natur.*, vol. 120, pp. 787-815, 1982.
- [10] T. L. Vincent and H. R. Pulliam, "Evolution of life history strategies for an asexual annual plant model," *Theor. Pop. Biol.*, vol. 17, pp. 215-231, 1980.
- [11] M. Ziólko and J. Kozłowski, "Evolution of body size: An optimization model," *Math. Biosci.*, vol. 64, pp. 127-143, 1983.
- [12] N. Perrin and R. Sibly, "Dynamic models of energy allocation and investment," *Ann. Rev. Ecol. Syst.*, vol. 24, pp. 379-410, 1993.

## A Graphical Approach of the Spectral Theory in the (max,+) Algebra

Jean Mairesse

**Abstract**—In this paper, we study matrices in the (max,+) algebra. We introduce a new tool for describing the deterministic spectral behavior of matrices of size  $3 \times 3$ . It consists of a graphical representation of eigenvectors and domains of attraction in the projective space.<sup>1</sup>

#### I. INTRODUCTION

Discrete-events dynamic systems (DEDS's) are a common framework to represent communication or manufacturing networks. Petri nets, and more precisely event graphs, are an example of a formalism to study DEDS's. Event graphs model phenomena such as synchronization or blocking. They have a simple interpretation in a nonconventional algebra, the (max,+) algebra.

The spectral theory of matrices in the (max,+) algebra is now well known. It can be tracked back to [5] or [4]. One of the main differences with the classical spectral theory is that there is a unique eigenvalue for irreducible matrices. As a consequence, the main interest and difficulty is to study eigenvectors associated with the unique eigenvalue. For a timed event graph, the eigenvalue is exactly the mean cycle time (inverse of the throughput rate). On the other hand, eigenvectors are associated with quantities such as: number of tokens in a place, waiting times, or idle times. Multiple eigenvectors mean multiple possible regimes for these quantities.

In this paper, we present the classical spectral results under a new light. We develop a tool for describing the spectral behavior of matrices of size  $3 \times 3$ . It consists of a graphical representation of asymptotic regimes in a projective space.

#### II. THE (max,+) ALGEBRA

We consider systems whose dynamic behavior is driven by a recursive equation of the form

$$x_i(n+1) = \max_{1 \leq j \leq k} [A_{ij} + x_j(n)], \quad i = 1, \dots, k. \quad (1)$$

We allow  $A_{ij}$  to be equal to  $-\infty$ . Let us introduce some new notations.

**Definition 1 [(max,+) Algebra]:** We consider the semi-field  $(\mathbb{R} \cup \{-\infty\}, \oplus, \otimes)$ . The law  $\oplus$  is "max," and  $\otimes$  is the usual addition. We set  $\varepsilon = -\infty$  and  $e = 0$ . The element  $\varepsilon$  is neutral for the operation  $\oplus$  and absorbing for  $\otimes$ . The element  $e$  is neutral for  $\otimes$ . The law  $\oplus$  is idempotent, i.e.,  $a \oplus a = a$ .  $(\mathbb{R} \cup \{\varepsilon\}, \oplus, \otimes)$  is an idempotent semiring or dioid. It is usually referred to as the (max,+) algebra. We shall denote it by  $\mathbb{R}_{\max}$ . In the rest of the paper, the notations "+, ×" will stand for the usual addition and multiplication. We will write  $ab$  for  $a \otimes b$ , however, whenever there is no possible confusion. For example, for  $a \in \mathbb{R}$ ,  $a^d = a^{\otimes d} = d \times a$ .

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