

Individual Behavior and Population Dynamics¹

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Abstract

Differential equations have been used in population biology to describe dynamics of interacting populations since the pioneering work of Lotka and Volterra. However, most of the work on population dynamics does not take into consideration individual decisions of animals. In behavioral ecology it was shown that animals often behave in such a way which maximizes certain criterion like energy or nutrient intake. Typically, this criterion is related to reproduction of animals, thus to fitness. We show how the theory of optimal foraging may be included into models of population dynamics. Typically, this leads to discontinuous differential equations, or more generally, to differential inclusions. We will discuss a few biologically relevant examples together with the underlying mathematics.

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1 Introduction

Since the times of Lotka and Volterra, interactions among populations and evolution of ecological systems have been modelled by differential or difference equations. Typically, these models do not consider the individual decisions of animals which influence the population dynamics. Several experimental studies in behavioral ecology show that animals can make decisions with respect to their activities. For predators typical activity is foraging while for parasitoids it is laying eggs. Let us consider a predator which meets various types of prey. Upon an encounter with a prey, the predator has to decide whether to attack the prey or not. If the predator decides to attack then this increases the energy reserves of the predator provided the attack is successful, but the predator by attacking and handling the prey loses some time which could be used for searching for another, possibly more profitable type of prey. Thus for a predator there is a trade-off: *to attack the prey upon an encounter or to search for possibly more profitable prey?* This sort of reasoning leads to the optimal foraging theory, which is concerned with the composition of the diet of a predator, for a review see [24]. Optimal foraging theory is based on the assumption that the predators are maximizing the net rate of energy intake which leads in the case of two types of prey to maximization of

$$R = \frac{E}{T_s + T_h}, \quad (1)$$

where T_s stands for the total time spent by searching, T_h denotes the total time spent by handling and E is the net amount of energy gained in the total time $T = T_s + T_h$ by a single predator. By u_i we denote the probability that a predator will attack prey type i upon an encounter, x_i is the density of prey type i , $\lambda_i x_i$ is the encounter rate of a predator with the i -th type of prey when searching, e_i is the expected net energy gained from the i -th type of prey and h_i is the expected handling time spent with the i -th type of prey. Then

$$T_h = h_1 \lambda_1 x_1 u_1 T_s + h_2 \lambda_2 x_2 u_2 T_s \quad (2)$$

and

$$E = (u_1 \lambda_1 x_1 e_1 + u_2 \lambda_2 x_2 e_2) T_s.$$

The optimality criterion (1) becomes

$$R(u_1, u_2) = \frac{u_1 \lambda_1 e_1 x_1 + u_2 \lambda_2 e_2 x_2}{1 + u_1 \lambda_1 h_1 x_1 + u_2 \lambda_2 h_2 x_2}. \quad (3)$$

The derivation of (3) is based on Holling disc equation, see [13,24]. Based on maximization of (3) composition of the diet of a predator which depends on the ranking of different types of prey according to the ratios e_i/h_i is obtained. The main result of the optimal foraging theory which considers the densities of populations of prey to be fixed states that predators will always forage on the most profitable type of prey, i. e. the prey type with the highest ratio e_i/h_i . The other type of prey will be included into the diet of a predator only if the value of R will not decrease by doing so. Thus assuming that the first type of prey is more profitable than the second one, $u_1 = 1$ and u_2 is either zero or one depending on the parameters involved. This basic model goes back to Charnov and many others who elaborated it including some other phenomena that may influence the decision of the predator. We refer to [22,24] for more detailed information and extensive reference list.

A similar problem is the choice of the food patch by a predator. Assume that food is distributed in patches and predators are moving freely between these patches. Then the predator has to choose how long to stay in a particular patch. Assuming that predators are free to settle in any patch, travel time between patches is negligible, predators are omniscient and resource densities in patches remain constant in time lead to *ideal free distribution* [9,14] which describes the equilibrium distribution of the population of predators between the habitat patches. Assuming that each consumer tries to settle in the patch where its rate of food intake is maximized, this model predicts that at equilibrium, predators in all patches will experience the same rate of the food intake.

There is experimental evidence that in some cases animals behave approximately according to optimality criteria mentioned above. However, what optimality exactly means may depend on the *currency* through which optimality is expressed. In the theory of optimal foraging the word optimal may mean maximum nutrient, energy, food etc. acquisition per unit of time, for host-parasite systems it may mean the number of eggs laid per unit time. Quite often a simple currency like energy or nutrient is not enough to describe optimality, since it may happen that the optimal choice may be also the most dangerous for the animal. For example, the patch where energy acquisition is high may also be more dangerous to the predators than other patches. Thus there may be a trade-off between energy or nutrient intake and mortality rate, i. e. survival. This leads to a necessity for a more general notion of optimality which is achieved through *fitness* defined as the instantaneous rate of increase of the number of genotype

copies of the individual [23]. The evolutionary biology treats fitness as the most general criterion which evolution maximizes. Having defined the optimality criterion we may compute the *optimal strategy* of an individual by maximizing this criterion over the set of all possible strategies. We note that often the strategies are defined via probabilities, like in the above examples (probability of attacking a prey, probability of staying in a patch), thus $0 \leq u_i \leq 1$.

Up to now we were considering the behavior of a single *average* individual. In order to describe the population dynamics we have to define the dynamics of the densities of populations. We will consider a system consisting of two populations of prey and one population of predators. The densities of these populations are denoted by x_1, x_2, x_3 . Then we have

$$\begin{aligned} x_1(t+T) - x_1(t) &= x_1(t)g_1(x_1(t), x_2(t))T - \lambda_1 x_1(t)u_1(t)x_3(t)T_s, \\ x_2(t+T) - x_2(t) &= x_2(t)g_2(x_1(t), x_2(t))T - \lambda_2 x_2(t)u_2(t)x_3(t)T_s, \\ x_3(t+T) - x_3(t) &= e_1 \lambda_1 x_1(t)u_1(t)x_3(t)T_s + e_2 \lambda_2 x_2(t)u_2(t)x_3(t)T_s - \\ &\quad m x_3(t)T. \end{aligned}$$

From (2) we get

$$T_s = \frac{T}{1 + h_1 \lambda_1 x_1 u_1 + \lambda_2 x_2 u_2}$$

and by taking $T \rightarrow 0$ we get the following system of differential equations which describe the population dynamics:

$$\begin{aligned} x_1' &= x_1 g_1(x_1, x_2) - \frac{u_1 \lambda_1 x_1 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} \\ x_2' &= x_2 g_2(x_1, x_2) - \frac{u_2 \lambda_2 x_2 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} \\ x_3' &= \frac{u_1 e_1 \lambda_1 x_1 x_3 + u_2 e_2 \lambda_2 x_2 x_3}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} - m x_3. \end{aligned} \quad (4)$$

The functions g_i are growth rate functions for populations of prey. According to the definition, the fitness function is given by the per capita growth rate of a predator, i. e.

$$\frac{u_1 e_1 \lambda_1 x_1 + u_2 e_2 \lambda_2 x_2}{1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2} - m \rightarrow \max, \quad (5)$$

see [18]. Following the optimal foraging theory we have to maximize (5) over all possible strategies, i. e. over all u_1, u_2 . We note that due to the

fact that the mortality rate m is independent from the foraging behavior of predators, maximization of (5) is equivalent to maximization of energy intake.

Similarly, we may derive a system of equations describing the dynamics of the patch model which gives

$$\begin{aligned}x_1' &= r_1(x) - \frac{\lambda_1 x_1 u_1}{1 + h_1 \lambda_1 x_1} x_3 \\x_2' &= r_2(x) - \frac{\lambda_2 x_2 u_2}{1 + h_2 \lambda_2 x_2} x_3 \\x_3' &= \left(\frac{e_1 \lambda_1 x_1}{1 + h_1 \lambda_1 x_1} - m_1 \right) u_1 x_3 + \left(\frac{e_2 \lambda_2 x_2}{1 + h_2 \lambda_2 x_2} - m_2 \right) u_2 x_3,\end{aligned}\tag{6}$$

see [6,17,19]. Here we assume that the mortalities of predators in patches may be different. The optimality criterion to maximize is

$$\left(\frac{e_1 \lambda_1 x_1}{1 + h_1 \lambda_1 x_1} - m_1 \right) u_1 + \left(\frac{e_2 \lambda_2 x_2}{1 + h_2 \lambda_2 x_2} - m_2 \right) u_2 \rightarrow \max.\tag{7}$$

Now we want to define the set of all possible strategies of a predator. In the case when predators decide whether to feed on a prey upon an encounter or not the set of possible strategies is given by

$$U_1 = \{(u_1, u_2) \mid 0 \leq u_1 \leq 1, 0 \leq u_2 \leq 1\}.\tag{8}$$

Here $u_i = 1$ means that upon an encounter with prey type i the predator will always attack this prey type while $u_i = 0$ means that predator will not attack the prey upon an encounter. In the case of patch selection the set of all possible controls is smaller

$$U_2 = \{(u_1, u_2) \mid 0 \leq u_1 \leq 1, 0 \leq u_2 \leq 1, u_1 + u_2 = 1\},\tag{9}$$

since now u_i , $i = 1, 2$ is the probability that a predator will stay in patch i and these two events are mutually exclusive. In order to get *optimal strategy* we have to maximize (5) or (7) either over U_1 or U_2 . The set of all controls which maximize the optimality criterion is called *the optimal strategy map*, since it depend on the state of the system $x = (x_1, x_2, x_3)$. Namely, if we denote by $S_1(x)$ the set of those controls which maximize (5) over U_1 and $S_2(x)$ the set of those controls which maximize (7) over U_2 we

get that

$$S_1(x) = \begin{cases} (1, 1) & \text{if } x_1 < \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \\ (1, 0) & \text{if } x_1 > \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \\ (1, u_2), 0 \leq u_2 \leq 1 & \text{if } x_1 = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}. \end{cases} \quad (10)$$

Thus there is a critical density of x_1 given by

$$x_1^* := \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \quad (11)$$

such that if $x_1 > x_1^*$ then each predator will forage exclusively on prey type 1, while if $x_1 < x_1^*$ then prey type 2 will be included into the diet of predators. If $x_1 = x_1^*$ then the optimal control is not uniquely given, i. e. $u_2 \in [0, 1]$. We set

$$M_1 = \{x \in \mathbf{R}^3 \mid x_1 = x_1^*\}.$$

In the case of the patch selection the strategy map is

$$S_2(x) = \begin{cases} (1, 0) & \text{if } x_1 > \frac{e_2 \lambda_2 x_2}{e_1 \lambda_1 + \lambda_1 \lambda_2 x_2 (e_1 h_2 - e_2 h_1)} \\ (0, 1) & \text{if } x_1 < \frac{e_2 \lambda_2 x_2}{e_1 \lambda_1 + \lambda_1 \lambda_2 x_2 (e_1 h_2 - e_2 h_1)} \\ (u_1, 1 - u_1) & \text{if } x_1 = \frac{e_2 \lambda_2 x_2}{e_1 \lambda_1 + \lambda_1 \lambda_2 x_2 (e_1 h_2 - e_2 h_1)}. \end{cases} \quad (12)$$

We set

$$M_2 = \{x \in \mathbf{R}^3 \mid x_1 = \frac{e_2 \lambda_2 x_2}{e_1 \lambda_1 + \lambda_1 \lambda_2 x_2 (e_1 h_2 - e_2 h_1)}\}.$$

We see that for both optimal foraging and patch selection the strategy map S_i is set-valued along a manifold M_i of a lower dimension. According to the assumption on optimal behavior of animals only those controls which satisfy

$$u \in S_i(x), \quad i = 1, 2 \quad (13)$$

are employed by predators. Thus it is not immediately clear whether solutions of (4) and (6) which obey (13) do exist and whether they are unique, since the control depends on the state of the system.

One of the reasons why it is important to include individual behavior in models of population dynamics is to study the effect of the individual behavior on the dynamical properties of the system. Namely, we may be interested in questions like: *Does optimal behavior stabilize predator-prey dynamics* or *Does optimal behavior promote the permanence of predator-prey systems*, (for permanence see [12]). In population biology mechanisms based on the density dependence have been thoroughly studied with respect to stability of systems. However, we may ask if individual behavior of animals itself may lead to stabilization (or permanence) of otherwise unstable systems. In [11] it was shown that strong aggregation of predators in more profitable patches may have stabilizing effect on Nicholson-Bailey model, which is otherwise unstable.

The influence of individual behavior on population dynamics was not studied systematically until recently. This is mainly due to the fact that straightforward extension of standard models of *static optimal foraging theory* like above examples show lead on population level to models which are not described by a differential equations with continuous right hand-side. Typically, the optimality criterion leads to controls which are not uniquely defined, thus on population level to *differential inclusions*. Some attempts have been made to approximate the step function which appears in the resulting differential inclusion by a continuous approximation, see [10] but the resulting systems are often so complex that non-trivial analysis is impossible. On the other hand the theory of differential inclusions and set-valued maps [1,2,7,8] allows to treat effectively models based on differential inclusions. In this review we want to show how these techniques may be applied in theoretical population biology to models which include individual decisions. We will be mainly concerned with the two previously mentioned examples, which are probably the most typical ones. However, several other examples in the context of host-parasitoid systems may be given, see [20]. This review is based on the work given in [4,6,15,16,17,18,19].

We want to mention that there exists another approach to model optimal decisions of animals which is based on the dynamic programming approach, for a review see [22]. This approach is more complex than the original Charnov model, since it allows to describe short term (daily) behavior of animals, which is based on the animal's bodily energy reserves. This model does not work with average animals like the above mentioned model of Charnov, but the behavior of animals within a population may differ in dependence on the current state of the animal.

2 Existence and Uniqueness of Solutions

In this part we want to review some basic mathematical results concerning the existence and uniqueness of solutions of differential equations which are applied in the models of population biology already mentioned. In general, the dynamics of interacting populations is described by a differential equation

$$x'(t) = f(x(t), u(t)) \quad (14)$$

where u is the control from a given set U of admissible controls. Together with (14) there is a set-valued map S which associates to any x a subset $S(x)$ of U . We will assume that the map S is set-valued only along a manifold M of a lower dimension, since this is always so in the above mentioned applications. Thus we have together with (14)

$$u(t) \in S(x(t)). \quad (15)$$

Solutions of (14), (15) are couples $(x(t), u(t))$ where x is an absolutely continuous function which satisfies (14) almost everywhere and u is a measurable function which satisfies (15) everywhere, see [2,7,8]. The above system may be seen either as a differential inclusion or, equivalently, as a Filippov solution of a differential equation with discontinuous right-hand side, see [8]. Indeed, the above system is equivalent to the following differential inclusion

$$x' \in F(x) := f(x, S(x)), \quad (16)$$

see [2]. Since S is single-valued with the exception of points belonging to the set M which has lower dimension, (14) is a single-valued differential equation at points which do not belong to the set M . The right-hand side of (14) cannot be continuously defined at points of M , thus we may consider (14) as a differential equation with a discontinuous right-hand side. The Filippov solution of such an equation is then defined as a solution of (16), see [8]. Since we are dealing with differential inclusion (16) we have to ask under which conditions solutions exist. We give here two results which apply in several cases of practical interest.

Proposition 1 ([6]) *Let $f : \mathbb{R}^n \times U \rightarrow \mathbb{R}^n$ be a continuous map which is linear in u . If the strategy map S has closed graph and non empty convex values, then for any initial condition (t_o, x_o) there exist a (strictly) positive T , an absolutely continuous $x : [t_o, t_o + T] \rightarrow \mathbb{R}^n$ and a bounded measurable $u : [t_o, t_o + T] \rightarrow U$ that satisfy (14), (15).*

This result may be applied to get existence of solutions of (6), but it does not apply to (4), since controls do not enter the dynamics described by (4) linearly. Below we give another result which may be applied also to (4).

In several cases solutions of (16) will be uniquely given despite the non-uniqueness in the right handside. In general, right uniqueness follows from one-sided Lipschitz condition, namely

$$\langle f_1 - f_2, x_1 - x_2 \rangle \leq L \|x_1 - x_2\|^2, \text{ for every } f_i \in F(x_i), i = 1, 2,$$

where L is a Lipschitz constant and $\langle \cdot, \cdot \rangle$ stands for the scalar product in \mathbf{R}^n , see [8]. This condition may not be easy to verify, but if we assume that M splits \mathbf{R}^n into two parts that we denote by G_1 and G_2 , like in the above examples then right uniqueness follows from Proposition 2 below. We denote by u_i the unique value of the control u in G_i . Let $f_i(x)$ denote the unique value of (14) for $x \in G_1$ and similarly for $f_2(x)$. For x such that $x \in M$, $f_1(x)$ denotes the limit of f_1 at the point x from the region G_1 and similarly for f_2 . By $n(x)$ we denote the normal to M at x oriented from G_2 towards G_1 .

Proposition 2 ([6]) *Let M be a C^2 manifold, and the vector $f_1(t, x) - f_2(t, x)$ be in C^1 . If for each point $x \in M$ at least one of the inequalities $\langle n(x), f_2(x) \rangle > 0$ or $\langle n(x), f_1(x) \rangle < 0$ is fulfilled, then right uniqueness for (14) holds.*

If f is not linear in u the existence and uniqueness of solutions of (14) may still be proved. For $x \in M$ we assume that $S(x)$ is an interval with the endpoints u_i .

Proposition 3 ([6],[8]) *Let M be a C^2 manifold, and moreover*

$$f, \frac{\partial f}{\partial u}, u_i \in C^1$$

and

$$\frac{\partial \langle n, f(x, u) \rangle}{\partial u} \neq 0 \text{ for all } u \in S(x).$$

If for each $t \in \mathbf{R}_+$ at each point $x \in M$ at least one of the inequalities $\langle n(x), f_2(t, x) \rangle > 0$ or $\langle n(x), f_1(t, x) \rangle < 0$ is fulfilled, then for each initial condition there exists a unique solution of (16).

Since Proposition 3 does not require the map $f(x, u)$ to be linear in u it may be applied to (4). Thus using the above Propositions we get that for any initial condition there exists a unique solution of (4) and (6) which satisfy $u_i \in S_i(x)$, see [6,18].

Qualitative analysis of differential equations with discontinuous right handside or differential inclusions is more difficult than the analysis of continuous differential equations. However, methods based on Lyapunov functions are still applicable to detect ω -limit sets, see [2,8]. This method proved to be useful in the case when the handling times equal zero, since this lead to discontinuous differential equations of Lotka-Volterra type for which Lyapunov function may be constructed, see [3,4].

For differential inclusions or differential equations with discontinuous right handside numerical approaches which are based on classical Euler or Runge-Kutta methods may not give satisfactory results since they lead typically to rapid oscillations. Thus, it is necessary to take very small step size in order to get a reasonable approximation of the exact solution. For systems like (4), (6) methods for numerical solutions of differential-algebraic equations may be used, see [15,21].

3 Qualitative Analysis along the Discontinuity Manifold

In this part we will assume that M splits \mathbf{R}^n into two parts which are denoted by G_1 and G_2 . This is the case of both examples given in the Introduction. In G_i the dynamics is described by a differential equation with a smooth right handside. Thus methods of local analysis for differential equations with smooth right handsides do apply in G_i . We have to study the behavior of trajectories when they fall on the discontinuity manifold M . This behavior is given by projections of vector fields f_1 and f_2 on the normal vector n to M . We have to distinguish four possible cases :

- (i) $\langle n, f_1 \rangle < 0$, $\langle n, f_2 \rangle > 0$ which means that trajectories of (16) will stay in M
- (ii) $\langle n, f_1 \rangle > 0$, $\langle n, f_2 \rangle > 0$ which means that trajectories of (16) will pass through M in direction from G^2 to G^1
- (iii) $\langle n, f_1 \rangle < 0$, $\langle n, f_2 \rangle < 0$ which means that trajectories of (16) will pass through M in direction from G^1 to G^2

(iv) $\langle n, f_1 \rangle > 0$, $\langle n, f_2 \rangle < 0$ which means that trajectories of (16) which start on M will move either to G^1 or to G^2 .

If the assumptions of Proposition 2 or 3 are fulfilled it follows that the case (iv) cannot happen. Under the conditions (ii) and (iii) the control will discontinuously change as the corresponding trajectory passes through M . This corresponds to sudden change in the behavior of animals, which is often called *switching*. Under the condition (i) a trajectory which hits M stays there as long as (i) holds. Such behavior is called *sliding regime* in the theory of discontinuous differential equations. If the system is in the part of M where sliding regime holds we may derive uniquely values of the control. For this let us assume that

$$M = \{x \in \mathbf{R}^n \mid h(x) = 0\}.$$

Then the control which governs the dynamics in sliding regime can be computed from the equation

$$\langle h'(x), f(x, u) \rangle = 0. \quad (17)$$

We will illustrate the above concepts on the model for patch selection [6]. In order to simplify the analysis we will assume that the mortality for predators in both patches are same ($m_1 = m_2 = m$) and handling times are zero ($h_1 = h_2 = 0$). Thus the dynamics of (6) is described by a discontinuous differential equation of Lotka-Volterra type:

$$\begin{aligned} x_1' &= a_1 x_1 - \lambda_1 x_1 u_1 x_3 \\ x_2' &= a_2 x_2 - \lambda_2 x_2 u_2 x_3 \\ x_3' &= e_1 \lambda_1 x_1 u_1 x_3 + e_2 \lambda_2 x_2 u_2 x_3 - m x_3 \end{aligned} \quad (18)$$

where the discontinuity plane M_2 is given by

$$M_2 = \{(x_1, x_2, x_3) \mid e_1 \lambda_1 x_1 = e_2 \lambda_2 x_2\}.$$

We assume $a_1 \geq a_2$. Then the subset of M where sliding regime appears is the set

$$M_s = \{(x_1, x_2, x_3) \mid x_3 > \frac{a_1 - a_2}{\lambda_1}\}.$$

In M_s , using (17) we may compute uniquely the control which governs the dynamics to be

$$u_1 = \frac{a_1 - a_2 + \lambda_2 x_3}{(\lambda_1 + \lambda_2) x_3}.$$

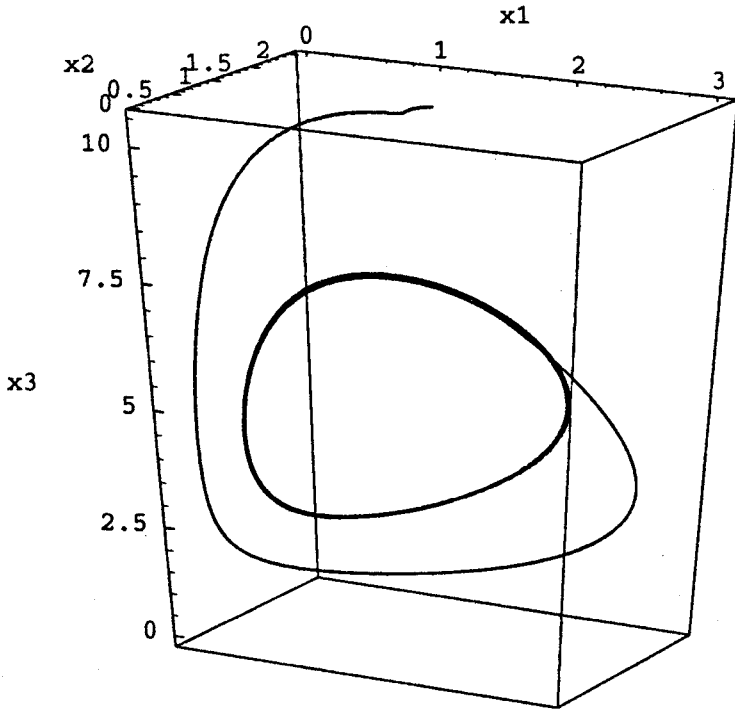


Figure 1: Solution of (18) with $a_1 = 3.5$, $a_2 = m = \lambda_1 = \lambda_2 = e_1 = e_2 = 1$.

Thus in M_s the dynamics is given by a Lotka-Volterra differential equation

$$\begin{aligned}
 x_1' &= Ax_1 - Kx_1x_3 \\
 x_2' &= Ax_2 - Kx_2x_3 \\
 x_3' &= (e_1\lambda_1x_1 - m)x_3
 \end{aligned} \tag{19}$$

where

$$A = \frac{a_1\lambda_2 + a_2\lambda_1}{\lambda_1 + \lambda_2}, \quad K = \frac{\lambda_1\lambda_2}{\lambda_1 + \lambda_2}.$$

Moreover, using Lyapunov function [3,4] it can be proved that for any initial condition the ω -limit set is the largest Lotka-Volterra cycle of (19)

which is in M_s , see Fig. 1. We note that the model described by (18) for fixed u_1, u_2 (i. e. when predators move between patches randomly) is not permanent since the weaker prey is eliminated from the system. However, we see that the optimal behaviour of predators leads in this example to permanence of the system, i. e. both prey types will survive indefinitely.

The dynamics of the model of optimal foraging (4) with the growth rate functions given by

$$g_i(x) = a_i \left(1 - \frac{x_i}{K_i}\right).$$

was discussed in [18]. We note that this model cannot be simplified by setting handling times to be zero, since by doing so we get that the optimal strategy of a predator is to attack a prey upon each encounter which leads to $u_1 = u_2 = 1$. In general, the behavior of (4) is quite complex. A partial analysis for $a_1 = a_2$, $\lambda_1 = \lambda_2$ shows that the effect of optimal foraging on population dynamics is quite complex and may be either stabilizing or destabilizing depending on values of parameters involved, see [18].

4 Discussion

In this review paper we wanted to show how powerful methods of the theory of differential inclusions may be used to model the population dynamics which include the individual behavior of individuals. The described approach may be used in a variety of examples that arise in theoretical population biology. The results based on the investigation of the appropriate models may shed some light on the effect of individual behavior on the dynamics of populations.

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