Lyapunov functions for Lotka–Volterra predator–prey models with optimal foraging behavior

David S. Boukal, Vlastimil Křivan

Department of Theoretical Biology, Institute of Entomology, Academy of Sciences of the Czech Republic, and Faculty of Biological Sciences USB, Branišovská 31, 370 05 České Budějovice, Czech Republic. e-mail: boukal@entu.cas.cz; krivan@entu.cas.cz

Abstract. The theory of optimal foraging predicts abrupt changes in consumer behavior which lead to discontinuities in the functional response. Therefore population dynamical models with optimal foraging behavior can be appropriately described by differential equations with discontinuous right-hand sides. In this paper we analyze the behavior of three different Lotka–Volterra predator–prey systems with optimal foraging behavior. We examine a predator–prey model with alternative food, a two-patch model with mobile predators and resident prey, and a two-patch model with both predators and prey mobile. We show that in the studied examples, optimal foraging behavior changes the neutral stability intrinsic to Lotka–Volterra systems to the existence of a bounded global attractor. The analysis is based on the construction and use of appropriate Lyapunov functions for models described by discontinuous differential equations.

Key words: Population dynamics – Optimal foraging – Global asymptotic stability – Filippov solutions – Lyapunov functions – LaSalle invariance principle

1. Introduction

Lotka–Volterra one-predator-one-prey type differential equations have played a prominent role in theoretical population biology. This is mainly due to the fact that for such equations one may find the first integral as well as Lyapunov functions which allow for global analysis of the model. However, when examining more complicated cases where

there are more food types available for predator, or where there are more predator types feeding on a particular prey type, classical Lotka–Volterra equations do not reflect the consequences of adaptive behavior of individuals. Standard models of optimal foraging theory such as prey and patch models assume that animals are perfect optimizers maximizing a quantity (e.g., the rate of energy intake) which is directly related to the fitness [14]. The basic prey–choice paradigm assumes that prey are homogeneously distributed across the space and predators encounter various prey types sequentially; such a model addresses the question whether a predator should attack a prey upon an encounter. The basic patch paradigm assumes that prey are distributed in patches and asks how long a predator should stay in a patch. Both types of models are examined in examples given in this paper.

Introducing optimal individual behavior in population dynamics often leads to differential inclusions [1, 2, 6, 7] rather than to differential equations due to the non-uniqueness of the optimal strategy [5]. For example in [9] and [11], the influence of optimal foraging on the dynamics of a system consisting of one predator type feeding on two prey types was studied. Following the optimal foraging theory [4] it was assumed there that when the density of the more profitable prey type decreases under a certain threshold, the less profitable prey type will be included in the predator's diet. This phenomenon leads to the non-uniqueness in the functional response, because optimal strategy at the moment of inclusion of the latter prey in the diet is not uniquely defined by maximization of the optimality criterion. Due to the appearance of the Holling type II functional response, global stability analysis of such a model was not possible but several biologically relevant observations relating to the stability, persistence and partial preferences were obtained. In this paper we will study a simpler model which assumes that the density of the alternative food type is constant. Such a model was introduced in [18]. Based on numerical simulations it was suggested there that the presence of the alternative food may lead to the persistence of predator–prey dynamics which would be otherwise violated. In this paper we show that under certain conditions the above model leads to a Lotka–Volterra type differential inclusion which may be globally studied using an appropriate Lyapunov function.

A similar situation appears when we study the dynamics of a predator population in a patchy environment [10]. Assuming that each predator settles in the patch where its rate of energy intake is maximized leads to switching sensu Murdoch [12, 13]. The distribution of predators at equilibrium where they will experience the same energy

intake in all patches is called "ideal free distribution" [8]. This model again leads to a Lotka–Volterra type differential inclusion and may be globally studied via an appropriate Lyapunov function. Following [10] we will also give a Lyapunov function for the case where not only predators but also prey are free to move between patches.

In mathematical language, the dynamics of the above models is typically described by a system of differential equations whose right-hand sides are set valued along a smooth manifold of codimension one. For such a type of differential inclusions, theorems ensuring existence and uniqueness of solutions were given in [7]; special cases arising in food web models were also treated in [5]. However, global qualitative analysis of such models is rather complicated due to the discontinuity of right-hand sides. Despite this fact, qualitative methods which are based on the use of an appropriate Lyapunov function can be implemented (see, e.g., [1] and [7] for general theory).

2. Stability results

In this section we recall some basic facts concerning discontinuous differential equations and stability. We also state the LaSalle invariance principle that will enable us to examine the models given in following sections. Various other versions of the LaSalle invariance principle were formulated for discontinuous differential equations [7, 15, 16]. We refer the reader to the Appendix for proofs of the propositions given in this and subsequent sections.

We will consider the autonomous Cauchy problem

$$\begin{aligned} \dot{x}(t) &= f(x(t)) \\ x(0) &= x_0 \in \mathbf{R}^n_+, \end{aligned} \tag{1}$$

where $\mathbf{R}^n_+ = \{x \in \mathbf{R}^n | x_1 > 0, \ldots, x_n > 0\}$, and a finite set of smooth, pairwise disjunct, open manifolds M^i, $i \in I$ (where I is a given index set) that divide the state space $\mathbf{R}^n_+$ in pairwise disjunct, open regions $G^j, j \in J$, and continuous vector fields $f^j\colon \overline{G^j} \to \mathbf{R}^n$ such that $f = f^j$ on G^j.

Because of the piecewise definition, f is not continuous and (1) may not have a solution. Filippov defined solutions of (1) as solutions of the differential inclusion

$$x'(t) \in K(x(t)), \tag{2}$$

where

$$K(x) = \bigcap_{\delta > 0} \bigcap_{\mu N = 0} \overline{\mathrm{co}}\, f(B(x; \delta) \backslash N).$$

Here *co* stands for the convex hull, $B(x; \delta)$ is the open δ-neighbourhood of x, and μ denotes the Lebesgue measure; see also [7], p. 85. Solutions of (2) are called Filippov solutions of (1). In this paper "solution" always means a Filippov solution.

Due to its definition, the set-valued map K is upper semicontinuous with non-empty compact convex values; consequently, (2) has at least one solution [7]. In general there may be more solutions of (2); uniqueness of solutions follows if, e.g., K satisfies a one-sided Lipschitz condition. In all examples considered in this paper, the solutions of the Cauchy problem (1) are unique and defined for all $t \geqq 0$.

We denote the solution of (1) by ξ_{x_o} and the ω-limit set of a given x_0 by $\omega^+(x_0)$. Moreover $\mathscr{S}^+(G) := \bigcup_{t \geqq 0} \mathscr{A}_G(t)$ (where $\mathscr{A}_G(t) = \{x \in \mathbf{R}^n_+ | x = \xi_{x_o}(t)$ for some $x_0 \in G\}$ is the attainable set) denotes the positive image of $G \subset \mathbf{R}^n_+$.

By the term *sliding domain* we denote a (connected) set S, $S \subset M^i$ for some $i \in I$, such that for all $x_0 \in S$, $\inf\{\tau \geqq 0 | \xi_{x_o}$ leaves the manifold M^i at time $\tau\} > 0$, i.e., once a solution enters a sliding domain, it stays there (at least locally) and follows the *sliding mode*.

The three basic types of solutions behavior along a single discontinuity manifold (that is the transversal motion with solutions passing from one region G^i to another, the sliding mode, and the case of non-unique solutions) are summarized in Fig. 1.

In order to determine the behavior of trajectories along M analytically, we take a vector n normal to M and oriented in direction from G^1 towards G^2 and we examine the scalar products of this vector with f^1 and f^2. Generically, there are three possibilities for the behavior of trajectories of (1) when they fall on M:

(i) $\langle n, f^1 \rangle < 0$, $\langle n, f^2 \rangle < 0$ (or $\langle n, f^1 \rangle > 0$, $\langle n, f^2 \rangle > 0$), and trajectories of (1) will pass through M in direction from G^2 to G^1 (or from G^1 to G^2); see Fig. 1 (Transversal motion)

(ii) $\langle n, f^1 \rangle > 0$, $\langle n, f^2 \rangle < 0$, and trajectories of (1) will stay in M; see Fig. 1 (Sliding mode)

(iii) $\langle n, f^1 \rangle < 0$, $\langle n, f^2 \rangle > 0$ which means that trajectories of (1) starting on M can move either to G^1 or to G^2; see Fig. 1 (Non–uniqueness).

We remark that the case (iii) of non-unique solutions does not occur in our examples.

We will use the following notion of a Lyapunov function:

Definition 1. *A function $V \in C^1(\mathbf{R}^n_+)$ is called a Lyapunov function of* (1) *on $\Omega \subset \mathbf{R}^n_+$ if it is non-negative on Ω and for all $x \in \Omega$*

$$\dot{V}^\star(x) := \max_{\eta \in K(x)} \langle \nabla V(x), \eta \rangle \leqq 0.$$
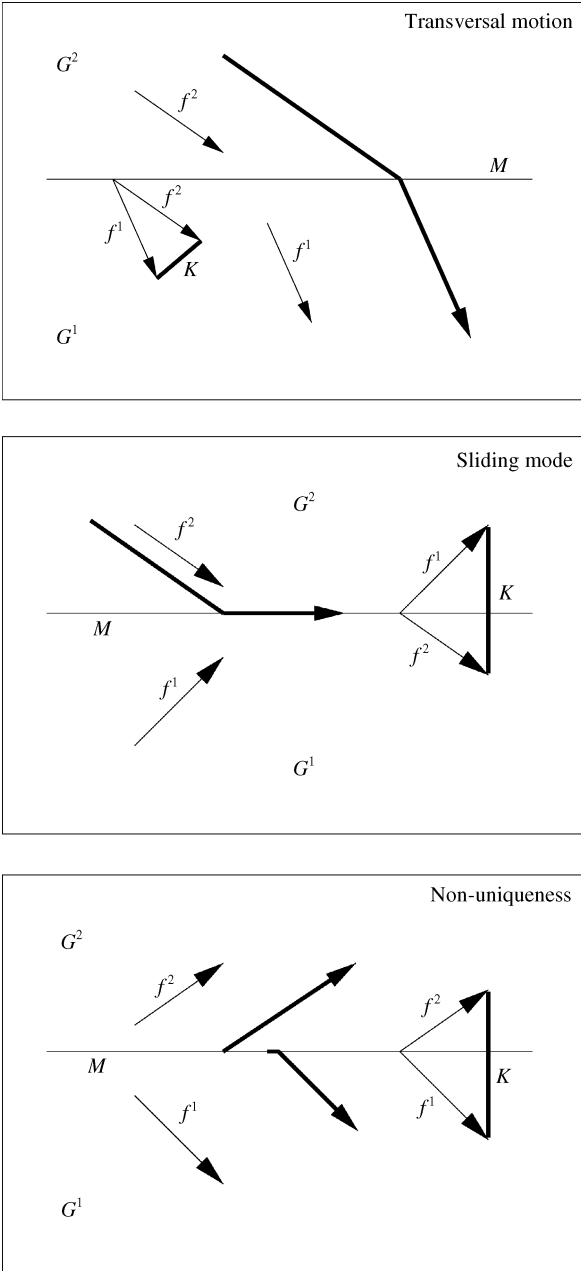
Fig. 1. Basic types of behavior along the discontinuity manifold. The discontinuity manifold M divides the state space in two regions, G^1 and G^2, with the respective vector fields f^1 and f^2. The set K is a convex combination of the two vectors at each point of M in this case. The bold arrows represent Filippov solutions. Note that in the case of non–unique trajectories, there are trajectories that leave each point of M to both G^1 and G^2.

We also define the following set attributed to a given Lyapunov function:

$$\Lambda = \Lambda(V, \Omega) := \{x \in \bar{\Omega} | \dot{V}^{\star}(x) = 0\}.$$

Remark. In the above definition, we assume for simplicity that V is differentiable because all Lyapunov functions we will construct satisfy this assumption. The case where V is Lipschitz (with some additional requirements) was treated in [16] and [7] while [15] treated the case where a Lyapunov function need not to be even continuous.

Proposition 1 (*LaSalle Invariance Principle*). *Let $G \subset \mathbf{R}_+^n$ be an open set satisfying*

$$\omega^+(G) := \bigcup_{x \in G} \omega^+(x) \subset \mathscr{S}^+(G)$$

and let every Filippov solution ξ_{x_o}, $x_0 \in G$, of (1) be unique and defined for all $t \geqq 0$. Let $V : \mathbf{R}_+^n \to \mathbf{R}$ be a Lyapunov function of (1) on $\mathscr{S}^+(G)$.
Then $\omega^+(G)$ is a subset of the largest positively invariant subset of $\bar{\Lambda}$.

Corollary 1. *Suppose that $\mathbf{R}_+^n \backslash G$ is repelling in the sense that all solutions exit $\mathbf{R}_+^n \backslash G$ in a finite time (i.e., for every $x_0 \in \mathbf{R}_+^n \backslash G$ exists $t(x_0) > 0$ such that for all $t \geqq t(x_0)$, $\xi_{x_o}(t) \in G$). Suppose further that G and $V : \mathbf{R}_+^n \to \mathbf{R}$ satisfy conditions of the above proposition, and that $\omega^+(\mathbf{R}_+^n) = \omega^+(G)$ is bounded.*
Then the set $\overline{\omega^+(\mathbf{R}_+^n)}$ is globally asymptotically stable (i.e., stable and a global attractor).

3. Predator–prey model with an alternative food

Let us consider one predator type feeding on two prey types. The density of the two prey types are denoted by x_1 and x_2 and the predator density is denoted by x_3, respectively. We will assume that foraging on the second prey type does not have any effect on its density, i.e., x_2 is constant through time. This may be the case of many arthropod predators when feeding on alternative food like pollen or honey dew. The first population is assumed to grow exponentially in the absence of predators. The dynamics of such a system can be described as follows:

$$x_1' = a_1 x_1 - \frac{p_1 \lambda_1 x_1 x_3}{1 + p_1 h_1 \lambda_1 x_1 + p_2 h_2 \lambda_2 K}$$

$$x_2' = 0$$

$$x_3' = \frac{p_1 e_1 \lambda_1 x_1 x_3 + p_2 e_2 \lambda_2 K x_3}{1 + p_1 h_1 \lambda_1 x_1 + p_2 h_2 \lambda_2 K} - m x_3,$$

see [18]. Here $x_2 = K$ is the constant density of prey type 2, p_i denotes the probability that a predator will attack prey type i upon an encounter, λ_i is the search rate of a predator for the i-th prey type, e_i is the expected net energy gained from the i-th prey type and h_i is the expected handling time spent with the i-th prey type. Setting handling time for the first prey to be zero ($h_1 = 0$) we get

$$x_1' = a_1 x_1 - \frac{p_1 \lambda_1 x_1 x_3}{1 + p_2 h_2 \lambda_2 K}$$

$$x_3' = \frac{p_1 e_1 \lambda_1 x_1 x_3 + p_2 e_2 \lambda_2 K x_3}{1 + p_2 h_2 \lambda_2 K} - m x_3. \tag{3}$$

Following the optimal foraging theory we assume that the control parameters p_1, p_2 are such that

$$\frac{x_3'}{x_3} \to \max. \tag{4}$$

Since we assume that $h_1 = 0$, it follows that the first prey type is more profitable for predators (the profitability is the energy/handling time ratio) and that it will always be included in the diet, i.e., $p_1 = 1$. The alternative prey type will be included in the predator's diet (i.e., $p_2 = 1$) only if

$$x_1 < x_1^\star := \frac{e_2}{\lambda_1 e_1 h_2}. \tag{5}$$

If $x_1 > x_1^\star$ then $p_2 = 0$, and if $x_1 = x_1^\star$ then p_2 may be anywhere in the interval $[0, 1]$. Thus p_2 as a function of the density of the first prey type is a step-like function and (3) is a differential inclusion [1, 2, 7].

Consequently, we split the (x_1, x_3) space in three parts: $G^1 := \{(x_1, x_3) | x_1 < x_1^\star\}$, $G^2 := \{(x_1, x_3) | x_1 > x_1^\star\}$ and $M := \{(x_1, x_3) | x_1 = x_1^\star\}$. Thus, if the state of the system is in G^1, the diet of predators will consist of both prey types while in G^2 it will consists only of the first, more profitable prey type. When the state of the system reaches M, the diet composition is not uniquely given by (4). The dynamics of the system in G^1 is described by

$$x_1' = a_1 x_1 - \frac{\lambda_1 x_1 x_3}{1 + h_2 \lambda_2 K}$$

$$x_3' = \frac{e_1 \lambda_1 x_1 x_3 + e_2 \lambda_2 K x_3}{1 + h_2 \lambda_2 K} - m x_3 \tag{6}$$

and in G^2 by

$$x_1' = a_1 x_1 - \lambda_1 x_1 x_3$$

$$x_3' = e_1 \lambda_1 x_1 x_3 - m x_3. \tag{7}$$

We note that both (6) and (7) are Lotka–Volterra equations if $e_2 < mh_2 + m/(\lambda_2 K)$.

Considering the scalar products of the vector $n = (1, 0)$ normal to M and oriented from G^1 towards G^2 with f^1 and f^2 (i.e., the right-hand sides of (6) and (7), respectively), we get that the system (3) driven by optimal foraging strategy possesses a unique trajectory for every initial condition [5, 7]. The sliding domain S is the interval

$$\{(x_1^\star, x_3) | q^1 := \frac{a_1}{\lambda_1} < x_3 < \frac{a_1}{\lambda_1}(1 + \lambda_2 K h_2) =: q^2\},$$

together with one or both endpoints depending on the sign of $mh_2 - e_2$.

The non-trivial equilibrium of (6) is

$$E^{(6)} = \left(\frac{m + \lambda_2 K(mh_2 - e_2)}{e_1 \lambda_1}, \frac{a_1}{\lambda_1}(1 + h_2 \lambda_2 K)\right)$$

and the non-trivial equilibrium of (7) is

$$E^{(7)} = \left(\frac{m}{e_1 \lambda_1}, \frac{a_1}{\lambda_1}\right).$$

We note that if $mh_2 > e_2$, both equilibria belong to G^2 while if $mh_2 < e_2 < mh_2 + m/(\lambda_2 K)$ they belong to G^1. Solutions leave the sliding domain S in one of the endpoints – either in $(x_1^\star, q^1)$, where $\langle n, f^2 \rangle = 0$, or in $(x_1^\star, q_2)$, where $\langle n, f^1 \rangle = 0$, depending on the sign of $mh_2 - e_2$. If $mh_2 = e_2$ then the equilibria $E^{(6)}$, $E^{(7)}$ belong to M and $S : E^{(7)}$ coincides with the lower end point $(x_1^\star, q^1)$ of the sliding domain S while $E^{(6)}$ coincides with the upper end point $(x_1^\star, q^2)$ of S. Since the dynamics in the sliding domain is described by $x_1' = 0$ we may compute the corresponding control p_2 which governs the dynamics in S and get:

$$\begin{aligned} x_1' &= 0 \\ x_3' &= \left(\frac{e_2}{h_2} - m\right) x_3. \end{aligned} \tag{8}$$

It follows from (8) that if $mh_2 = e_2$ then all points in S are equilibria for (3). If $mh_2 > e_2$ then trajectories in sliding domain move "downwards" (x_3 decreases) while if $mh_2 < e_2 < mh_2 + m/(\lambda_2 K)$ they move "upwards" (x_3 increases).

The global behavior of (3) is obtained from the knowledge of an appropriate Lyapunov function. We set

$$V_2(x_1, x_3) = e_1\lambda_1\left[-\frac{m}{e_1\lambda_1}\ln\left(\frac{e_1\lambda_1 x_1}{m}\right) + x_1 - \frac{m}{e_1\lambda_1}\right]$$

$$+ \lambda_1\left[-\frac{a_1}{\lambda_1}\ln\left(\frac{\lambda_1 x_3}{a_1}\right) + x_3 - \frac{a_1}{\lambda_1}\right]$$

and

$$V_1(x_1, x_3) = \frac{e_1\lambda_1}{1 + h_2\lambda_2 K}\left[-\frac{m + \lambda_2 K(mh_2 - e_2)}{e_1\lambda_1}\ln\left(\frac{e_1\lambda_1 x_1}{m + \lambda_2 K(mh_2 - e_2)}\right)\right.$$

$$\left. + x_1 - \frac{m + \lambda_2 K(mh_2 - e_2)}{e_1\lambda_1}\right] + \frac{\lambda_1}{1 + h_2\lambda_2 K}$$

$$\times\left[-\frac{a_1}{\lambda_1}(1 + h_2\lambda_2 K)\ln\left(\frac{\lambda_1 x_3}{a_1(1 + h_2\lambda_2 K)}\right)\right.$$

$$\left. + x_3 - \frac{a_1}{\lambda_1}(1 + h_2\lambda_2 K)\right].$$

Functions V_1 and V_2 are Lyapunov functions for differential equations (6) and (7) in the usual sense. Using these two functions we may construct (several) Lyapunov functions for (3) driven by optimal foraging strategy.

Proposition 2. *If $mh_2 > e_2$ then V_2 is a Lyapunov function on $\mathbf{R}_+^2$ for (3), and*

$$\omega^+(\mathbf{R}_+^2) = \{(x_1, x_3)|V_2(x_1, x_3) \leqq V_2(x_1^\star, q^1)\} \subset G^2 \cup (x_1^\star, q^1),$$

see Fig. 2A.
   If $mh_2 < e_2 < mh_2 + m/\lambda_2 K$ then V_1 is a Lyapunov function on $\mathbf{R}_+^2$ for (3), and

$$\omega^+(\mathbf{R}_+^2) = \{(x_1, x_3)|V_1(x_1, x_3) \leqq V_1(x_1^\star, q^2)\} \subset G^1 \cup (x_1^\star, q^2),$$
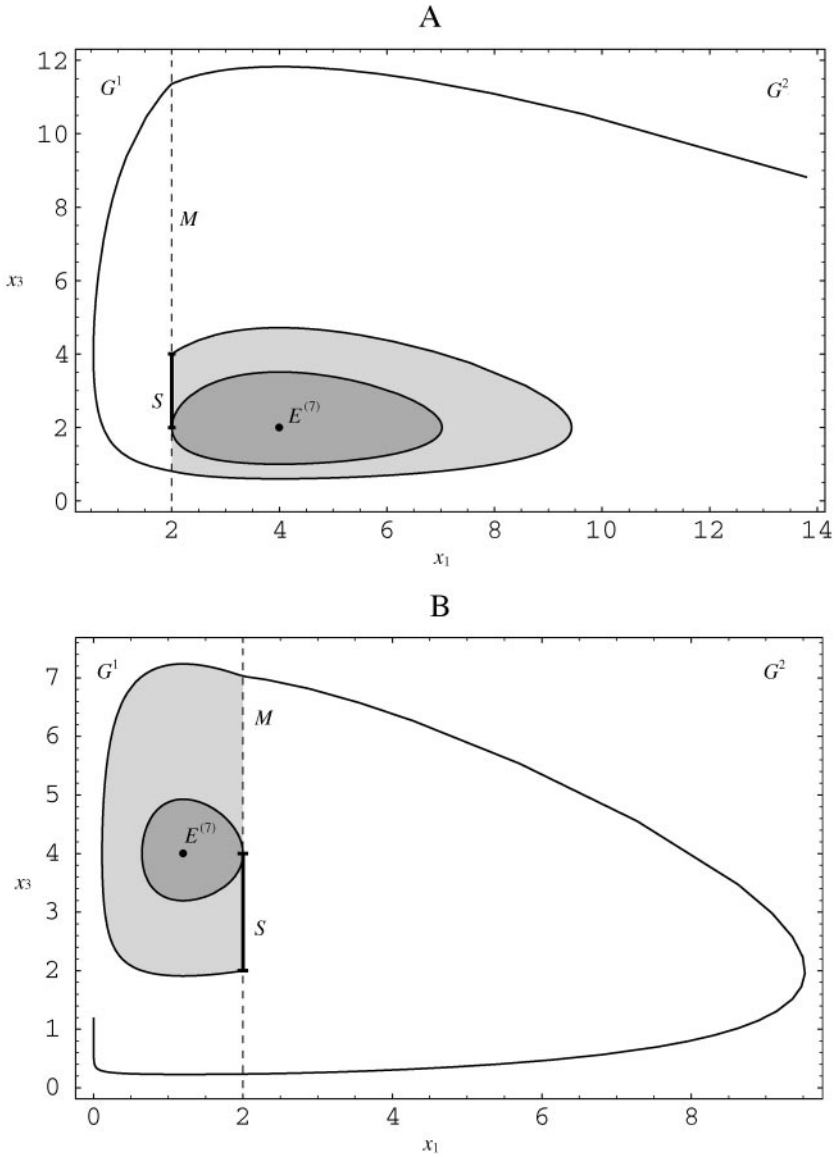
see Fig. 2B.
   If $mh_2 = e_2$ then $V_1 + V_2$ is a Lyapunov function on $\mathbf{R}_+^2$ for (3), and

$$\omega^+(\mathbf{R}_+^2) = S.$$

   Moreover the set $\omega^+(\mathbf{R}_+^2)$ is the global attractor for the system (3) in all three cases.

Remark. If $mh_2 > e_2$ (see Fig. 2A) the dimensionality of the state space ($n = 2$) also implies that trajectories cannot cross the largest invariant

Fig. 2. Dynamics of the predator–prey model (3) with a fixed density of the alternative food. In **A** parameters are such that $mh_2 > e_2$. Trajectory shown in the figure enters the sliding domain S in the point $(x_1^\star, q^2)$. Dark grey area denotes the global attractor $\omega^+(\mathbf{R}_+^2)$, middle grey area denotes the largest positively invariant set of $G^2 \cup M$. In **B** parameters are such that $mh_2 < e_2 < mh_2 + m/(\lambda_2 K)$. Trajectory shown in the figure enters the sliding domain S in the point $(x_1^\star, q^1)$. Dark grey area denotes the global attractor $\omega^+(\mathbf{R}_+^2)$, middle grey area denotes the largest positively invariant set of $G^1 \cup M$.

cycle [= border of the global attractor $\omega^+(\mathbf{R}_+^2)$] and for all initial conditions $x_0 \notin \omega^+(\mathbf{R}_+^2)$ thus holds:

$$\omega^+(x_0) \neq \partial(\omega^+(\mathbf{R}_+^2)) \equiv \{(x_1, x_3) | V_2(x_1, x_3) = V_2(x_1^\star, q^1)\}.$$

A similar statement holds for $mh_2 < e_2 < mh_2 + m/(\lambda_2 K)$, see Fig. 2B.

The biological interpretation of the dynamics yields the following results (see also [9], [11] and [18] for more discussion). If the alternative food is not sufficiently "attractive" or is "low-valued" for the predator ($m > e_2/h_2$, i. e., predator mortality is larger than the profitability of the second prey type), then no alterative food is taken after the transient period (see Fig. 2A) and we then observe a specialist predator. On the contrary, if the alternative food is "attractive" or "high-valued" but not "overcompensating" (with $e_2\lambda_2 K/(1 + h_2\lambda_2 K) < m < e_2/h_2$) then the alternative food is permanently included in the predator's diet in the limit behavior and the predator becomes a generalist (see Fig. 2B). In both cases, the system with initial conditions outside the global attractor always exhibits a finite period of transient behavior after which the solution enters its limit cycle – the largest Lotka–Volterra cycle that is contained in the invariant set Λ. Importantly, the presence of the alternative food leads to a partial stabilization of the system in the sense of reducing the amplitude of oscillations of solutions compared to the same system from which the alternative food would be taken out. In the singular case $m = e_2/h_2$, solutions also exhibit transient behavior but the solutions then enter a fixed point belonging to the manifold M in which a nontrivial portion ($0 < p_2 < 1$) of the alternative food is eaten by the (generalist) predator. Finally, if $m \leq e_2\lambda_2 K/ (1 + h_2\lambda_2 K)$, then the presence of the alternative food destabilizes the system. The predator mortality is overcompensated by the natality induced by the alternative food and consequently the prey x_1 dies out ($x_1 \rightarrow 0$) while the predator grows exponentially with $t \rightarrow +\infty$. Of course, for such parameter values the model would have to be altered to meet more realistic results, e.g., by changing the predator natality to a logistic function.

4. Patch model: only predators are free to move

Here we consider a system consisting of two prey patches, with predators moving freely between these two patches, the time of travel between patches being zero. Using the Lyapunov function approach, we are able to rigorously show the limiting behavior of the system announced in [10].

The dynamics of such a system after an appropriate rescaling can be described by the following system of differential equations:

$$x_1' = a_1 x_1 - \lambda_1 u_1 x_1 x_3$$

$$x_2' = a_2 x_2 - \lambda_2 u_2 x_2 x_3 \tag{9}$$

$$x_3' = (x_1 - m_1) u_1 x_3 + (x_2 - m_2) u_2 x_3.$$

Here x_1, x_2 are prey in patch 1 and 2, and x_3 is predator population abundance, respectively. We assume that $a_1 \geqq a_2$. Controls u_1, u_2 denote the fraction of a lifetime that a predator spends in patch 1 or in patch 2, respectively. Again we assume that predators are perfect optimizers, i.e., they maximize their instantaneous growth rate (4). The values of control are [10]:

$$(u_1, u_2) = \begin{cases} (1, 0) & \text{if } x_1 - m_1 > x_2 - m_2 \\ (0, 1) & \text{if } x_1 - m_1 < x_2 - m_2 \\ (u_1, u_2), u_1 + u_2 = 1 & \text{if } x_1 - m_1 = x_2 - m_2. \end{cases} \tag{10}$$

This means that if $x_1 - m_1 > x_2 - m_2$ then all predators aggregate in patch 1 while if $x_1 - m_1 < x_2 - m_2$ then all predators are in patch 2. If $x_1 - m_1 = x_2 - m_2$ then the exact distribution of the predator population between the two patches is not a priori given. The existence and uniqueness of solutions of (9) follows from [5].

Before applying the Proposition 1, we first determine the space structure and sliding domains of (9). We set

$$G^1 := \{(x_1, x_2, x_3) \in \mathbf{R}_+^3 | x_1 - m_1 > x_2 - m_2\}$$

$$G^2 := \{(x_1, x_2, x_3) \in \mathbf{R}_+^3 | x_1 - m_1 < x_2 - m_2\}$$

$$M := \{(x_1, x_2, x_3) \in \mathbf{R}_+^3 | x_1 - m_1 = x_2 - m_2\}.$$

We denote the right–hand side of (9) in G^i by $f^i(x)$, $i = 1, 2$.

We note that since the second population grows exponentially while the growth of the first and third one is bounded in G^1, solutions starting from G^1 must necessarily hit the set M. The same also holds when solutions start in G^2. In order to determine the sliding domain $S \subset M$, we take the vector $n = (1, -1, 0)$ which is perpendicular to M and oriented in direction from G^2 towards G^1 and get:

$$\langle n, f^1(x) \rangle = x_1(a_1 - a_2 - \lambda_1 x_3) - a_2(m_2 - m_1)$$

$$\langle n, f^2(x) \rangle = a_1 x_1 - (a_2 - \lambda_2 x_3)(m_2 - m_1 + x_1).$$

Thus

$$\langle n, f^2(x)\rangle > 0 \text{ if } x_3 > g_1(x_1) := \frac{x_1(a_2 - a_1) + a_2(m_2 - m_1)}{\lambda_2(x_1 + m_2 - m_1)}$$

$$\langle n, f^1(x)\rangle < 0 \text{ if } x_3 > g_2(x_1) := \frac{a_1 - a_2}{\lambda_1} + \frac{a_2(m_1 - m_2)}{\lambda_1 x_1}.$$

(11)

Both g_1 and g_2 are well defined, smooth functions on $\mathbf{R}_+$ since
on M we have $x_1 + m_2 - m_1 = x_2 > 0$. The interior of the sliding
domain is then the set $int S = \{x \in M | x_3 > \max\{g_1(x_1), g_2(x_1)\}\}$.
The behavior of trajectories on M depends on the relation between
m_1 and m_2.

If $m_1 > m_2$ then $g_2(x_1) > 0 > g_1(x_1)$ always holds since
$x_1 = x_2 + m_1 - m_2$, and consequently $\langle n, f^2\rangle > 0$ on M. For $x \in M$
there are the following possibilities (see Fig. 1A in [10]):

(i) If $x \in \overline{int S}$ then trajectory ξ_x (locally) stays in $int S$;
(ii) If $x \notin \overline{int S}$ (i. e., $x_3 < g_2(x_1)$) then ξ_x crosses M in direction from
     G^2 towards G^1;
(iii) If $x \in \partial S$, and $x_3 = g_2(x_1)$ then ξ_x either stays in $\overline{int S}$ or it enters G^1.

To show that on ∂S only (iii) may hold, we realize that $\langle n, f^2(x)\rangle > 0$
there; it follows that trajectories cannot enter G^2 at these points.

If $m_1 \leqq m_2$ then g_1 is decreasing while g_2 is increasing for $x_1 > 0$,
and the two functions intersect at the point

$$P_1 = \frac{a_2(m_2 - m_1)}{a_1 - a_2} > 0,$$

with $g_1(P_1) = g_2(P_1) = 0$. In this case the following behavior of trajec-
tories on M occurs (see Fig. 1B in [10]):

(i′) If $0 < x_3 < g_2(x_1)$ which can happen only if $x_1 > P_1$ then the
     corresponding trajectory crosses M in direction from G^2 towards
     G^1
(ii′) If $0 < x_3 < g_1(x_1)$ which can happen only if $0 < x_1 < P_1$ then the
     trajectory crosses M in direction from G^1 towards G^2
(iii′) If $x \in int S$ then the trajectory (locally) stays in $int S$.
(iv′) If $x \in \partial S$, $x_3 = g_2(x_1)$ and $x_1 > P_1$ then the trajectory either stays
     in $\overline{int S}$ or enters G^1
(v′) If $x \in \partial S$, $x_3 = g_1(x_1)$ and $x_1 < P_1$ then the trajectory either stays
     in $\overline{int S}$ or enters G^2.

We may compute the corresponding control in the sliding domain using $x_1' = x_2'$:

$$u_1(x_1, x_2, x_3) = \frac{a_1 x_1 + (m_1 - m_2 - x_1)(a_2 - \lambda_2 x_3)}{((\lambda_1 + \lambda_2)x_1 + \lambda_2(m_2 - m_1))x_3}.$$

The dynamics in the sliding regime is described by

$$\begin{aligned} x_1' &= \frac{x_1(m_1 - m_2 - x_1)(\lambda_1 \lambda_2 x_3 - a_1 \lambda_2 - a_2 \lambda_1)}{x_1(\lambda_1 + \lambda_2) + \lambda_2(m_2 - m_1)} \\ x_3' &= (x_1 - m_1)x_3 \end{aligned} \tag{12}$$

with the following non-trivial equilibrium

$$E^{(12)} = \left(m_1, m_2, \frac{a_2 \lambda_1 + a_1 \lambda_2}{\lambda_1 \lambda_2} \right).$$

We note that $E^{(12)} \in S$ regardless of the values of system parameters. The following proposition shows the global behavior of the system:

Proposition 3. *Function*

$$V(x_1, x_2, x_3) = \lambda_2 \left(x_1 - m_1 - m_1 \ln \frac{x_1}{m_1} \right) + \lambda_1 \left(x_2 - m_2 - m_2 \ln \frac{x_2}{m_2} \right)$$

$$+ \lambda_1 \lambda_2 x_3 - (a_1 \lambda_2 + a_2 \lambda_1) - (a_1 \lambda_2 + a_2 \lambda_1) \ln \frac{\lambda_1 \lambda_2 x_3}{a_1 \lambda_2 + a_2 \lambda_1}$$

is a Lyapunov function on $\mathbf{R}_+^3$ for (9), and $\omega^+(\mathbf{R}_+^3) = \{x \in S | \xi_x \text{ stays in } S\}$. Moreover the set $\overline{\omega^+(\mathbf{R}_+^3)}$ is the lobal attractor for the system (9).

It follows from $\langle \nabla V(x), \eta \rangle = 0$ for all $\eta \in K(x)$ and $x \in M$ that the set $\omega^+(\mathbf{R}_+^3)$ consists of closed cycles $V(x_1, x_2, x_3) = const$ which are contained in S.

Therefore we again see that the neutral stability of the classical Lotka–Volterra system is partially lost, since the ω-limit set cannot be outside the largest invariant cycle contained in S.

The situation is particularly simple when $m_1 = m_2 = m$. In this case

$$g_1(x_1) = \frac{a_2 - a_1}{\lambda_2} < 0, \quad g_2(x_1) = \frac{a_1 - a_2}{\lambda_1} > 0,$$

and (12) is a Lotka–Volterra equation. The (closed) set $\omega^+(\mathbf{R}_+^3) \subset S$ is then given by the largest Lotka–Volterra cycle of (12) which is not

below the line $x_3 = (a_1 - a_2)/\lambda_1$:

$$\omega^+(\mathbf{R}_+^3) := \left\{ (x_1, x_1, x_3) | x_1 - m\ln x_1 + \frac{\lambda_1 \lambda_2}{\lambda_1 + \lambda_2} x_3 - \frac{a_1 \lambda_2 + a_2 \lambda_1}{\lambda_1 + \lambda_2} \ln x_3 \right.$$

$$\left. \leqq m(1 - \ln m) + \frac{\lambda_2}{\lambda_1 + \lambda_2}(a_1 - a_2) - \frac{a_1 \lambda_2 + a_2 \lambda_1}{\lambda_1 + \lambda_2} \ln \frac{a_1 - a_2}{\lambda_1} \right\}.$$

In this case it is also easy to see that there are only two possibilities: either a trajectory falls at a certain moment in $\omega^+(\mathbf{R}_+^3)$ and then it follows the corresponding Lotka–Volterra cycle of (12), or it approaches the set $\omega^+(\mathbf{R}_+^3)$ from outside.

We briefly recall here that the optimal foraging of predators ensures the coexistence of all three species and again reduces oscillations of the underlying Lotka–Volterra model.

5. Patch model: both predators and prey are moving between two patches

Now we assume that both predators and prey are free to move between the two patches and their travel time is negligible. Such a system was described in [10] by the following system of differential equations:

$$x' = (a_1 - \lambda_1 u_1 y)v_1 x + (a_2 - \lambda_2 u_2 y)v_2 x$$
$$y' = (e_1 \lambda_1 v_1 x - m_1)u_1 y + (e_2 \lambda_2 v_2 x - m_2)u_2 y \tag{13}$$

$$u_1, v_1, u_2, v_2 \geqq 0, u_1 + u_2 = v_1 + v_2 = 1.$$

Again, we assume the densities x of prey and y of predator to have positive initial values and, without loss of generality, $a_1 \geqq a_2$. Controls u_1 and v_1 denote fractions of the population of predators and prey which are in the patch 1 at time t, respectively (similarly for u_2, v_2). Since for each population fitness is given by the instantaneous growth rate, this leads to maximization of

$$(a_1 - \lambda_1 u_1 y)v_1 + (a_2 - \lambda_2(1 - u_1)y)(1 - v_1) \to \max_{v_1},$$
$$(e_1 \lambda_1 v_1 x - m_1)u_1 + (e_2 \lambda_2(1 - v_1)x - m_2)(1 - u_1) \to \max_{u_1}, \tag{14}$$

in the sense of achieving Nash equilibrium. We recall that at the Nash equilibrium in a non-cooperative game, no individual can increase its fitness by changing its strategy unilaterally. A pair $(\tilde{u}_1, \tilde{v}_1)$ is therefore considered to be optimal if the following inequalities hold for all u_1

and v_1:

$$(e_1\lambda_1\tilde{v}_1 x - m_1)\tilde{u}_1 + (e_2\lambda_2(1-\tilde{v}_1)\, x - m_2)(1-\tilde{u}_1)$$

$$\geqq (e_1\lambda_1\tilde{v}_1 x - m_1)\, u_1 + (e_2\lambda_2(1-\tilde{v}_1)\, x - m_2)(1-u_1),$$

$$(a_1 - \lambda_1\tilde{u}_1 y)\tilde{v}_1 + (a_2 - \lambda_2(1-\tilde{u}_1)\, y)\,(1-\tilde{v}_1)$$

$$\geqq (a_1 - \lambda_1\tilde{u}_1 y)\, v_1 + (a_2 - \lambda_2(1-\tilde{u}_1)\, y)\,(1-v_1).$$

Provided $m_1 \geqq m_2$ the Nash equilibrium $N(x, y) = (\tilde{v}_1, \tilde{u}_1)$ for system (13) is [10]:

(1) $N(x, y) = (1, 0)$ if $x < x^\star$
(2) $N(x, y) = (1, 1)$ if $x > x^\star, y < y^\star$
(3) $N(x, y) = (v_1^\star, u_1^\star)$ if $x > x^\star, y > y^\star$
(4) $N(x, y) = \{(1, u_1)|u_1 \in [0, 1]\}$ if $x = x^\star, y \leqq y^\star$
(5) $N(x, y) = \{(1, u_1)|u_1 \in [0, u_1^\star]\}$ if $x = x^\star, \ y > y^\star$
(6) $N(x, y) = \{(v_1, 1)|v_1 \in [v_1^\star, 1]\}$ if $x > x^\star, \ y = y^\star$

where

$$x^\star = \frac{m_1 - m_2}{e_1\lambda_1}, \qquad y^\star = \frac{a_1 - a_2}{\lambda_1},$$

$$u_1^\star = \frac{a_1 - a_2 + \lambda_2 y}{(\lambda_1 + \lambda_2)y}, \qquad v_1^\star = \frac{m_1 - m_2 + e_2\lambda_2 x}{(e_1\lambda_1 + e_2\lambda_2)x}.$$

If $m_1 < m_2$, then the Nash equilibrium is:

(1′) $N(x, y) = (0, 1)$ if $x < x^{\star\star}, y > y^\star$
(2′) $N(x, y) = (1, 1)$ if $y < y^\star$
(3′) $N(x, y) = (v_1^\star, u_1^\star)$ if $x > x^{\star\star}, y > y^\star$
(4′) $N(x, y) = \{(v_1, 1)|v_1 \in [0, 1]\}$ if $x \leqq x^{\star\star}, y = y^\star$
(5′) $N(x, y) = \{(v_1, 1)|v_1 \in [v_1^\star, 1]\}$ if $x > x^{\star\star}, y = y^\star$
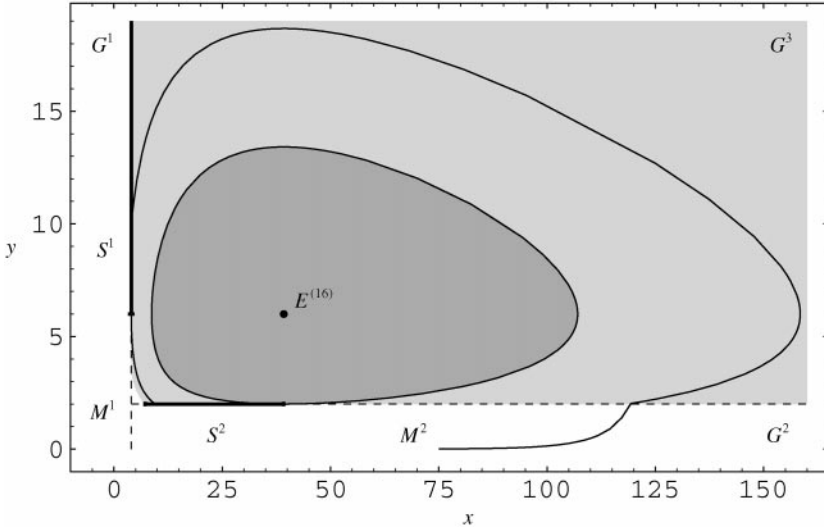(6′) $N(x, y) = \{(0, u_1)|u_1 \in [u_1^\star, 1]\}$ if $x = x^{\star\star}, y > y^\star$

where

$$x^{\star\star} = \frac{m_2 - m_1}{e_2\lambda_2}.$$

Let us first consider the case $m_1 \geqq m_2$. We set

$$G^1 := \{(x, y) \in \mathbf{R}_+^2 | x < x^\star\}$$

$$G^2 := \{(x, y) \in \mathbf{R}_+^2 | x > x^\star, y < y^\star\}$$

$$G^3 := \{(x, y) \in \mathbf{R}_+^2 | x > x^\star, y > y^\star\}$$

Fig. 3. Dynamics of the patch model (13) where both predators and prey behavior is adaptive. In this figure $m_1 > m_2$, and a trajectory that enters both sliding domains before following the largest invariant cycle in G^3 is shown. Dark grey area denotes the global attractor $\omega^+(\mathbf{R}^2_+)$, middle grey area denotes the largest positively invariant set of $G^3 \cup M^1 \cup M^2$.

$$M^1 := \{(x, y) \in \mathbf{R}^2_+ | x = x^\star\}$$

$$M^2 := \{(x, y) \in \mathbf{R}^2_+ | x > x^\star, y = y^\star\}$$

(G^1 and M^1 being empty for $m_1 = m_2$) and denote the righthand side of (13) in G^i, $i = 1, 2, 3$, by $f^i(x, y)$ (see Fig. 3).

Before constructing a Lyapunov function, we point out some properties of the system (13). All trajectories leave the region G^1 in a finite time as the system (13) takes in G^1 the following form:

$$\begin{aligned} x' &= a_1 x \\ y' &= -m_2 y. \end{aligned} \tag{15}$$

The system (13) turns in Lotka–Volterra equations both in G^2

$$\begin{aligned} x' &= (a_1 - \lambda_1 y)x \\ y' &= (-m_1 + e_1\lambda_1 x)y \end{aligned} \tag{16}$$

and in G^3

$$\begin{aligned} x' &= \left(\frac{a_1\lambda_2 + a_2\lambda_1}{\lambda_1 + \lambda_2} - \frac{\lambda_1\lambda_2}{\lambda_1 + \lambda_2}y\right)x \\ y' &= \left(-\frac{e_1\lambda_1 m_2 + e_2\lambda_2 m_1}{e_1\lambda_1 + e_2\lambda_2} + \frac{e_1\lambda_1 e_2\lambda_2}{e_1\lambda_1 + e_2\lambda_2}x\right)y. \end{aligned} \tag{17}$$

The respective nontrivial fixed points of the two systems

$$E^{(16)} = (x^{(16)}, y^{(16)}) = \left(\frac{m_1}{e_1\lambda_1}, \frac{a_1}{\lambda_1}\right)$$

$$E^{(17)} = (x^{(17)}, y^{(17)}) = \left(\frac{e_1\lambda_1 m_2 + e_2\lambda_2 m_1}{e_1\lambda_1 e_2\lambda_2}, \frac{a_1\lambda_2 + a_2\lambda_1}{\lambda_1\lambda_2}\right),$$

(18)

are both in G^3 as

$$x^{(17)} > x^{(16)} > x^\star$$
$$y^{(17)} > y^{(16)} > y^\star.$$

(19)

Moreover, there are two sliding domains

$$S^1 \subset M^1, S^1 := \{(x, y) | x = x^\star, y > y^{(17)}\}$$
$$S^2 \subset M^2, S^2 := \{(x, y) | y = y^\star, x^{(16)} \leqq x < x^{(17)}\}.$$

On S^1, we may derive from $x' = 0$ and $\tilde{v}_1 = 1$ that $(\tilde{u}_1, \tilde{v}_1) = (a_1/(\lambda_1 y), 1)$; similarly on S^2 we get $(\tilde{u}_1, \tilde{v}_1) = (1, m_1/(e_1\lambda_1 x))$. It follows that $y' = -m_2 y$ on S^1 and $x' = a_2 x$ on S^2. We denote the righthand side of (13) on S^i by f^{S^i}.

The situation is essentially the same in the case where $m_1 < m_2$. The state space $\mathbf{R}_+^2$ then decomposes as follows:

$$G^1 := \{(x, y) \in \mathbf{R}_+^2 | x < x^{\star\star}, y > y^\star\}$$
$$G^2 := \{(x, y) \in \mathbf{R}_+^2 | y < y^\star\}$$
$$G^3 := \{(x, y) \in \mathbf{R}_+^2 | x > x^{\star\star}, y > y^\star\}$$
$$M^1 := \{(x, y) \in \mathbf{R}_+^2 | x = x^{\star\star}, y > y^\star\}$$
$$M^2 := \{(x, y) \in \mathbf{R}_+^2 | y = y^\star\}.$$

Systems in G^2 and G^3 are again governed by the equations (16) and (17), respectively. The only differences are that the coefficients of the system (13) in G^1 are different from those of (15):

$$x' = a_2 x$$
$$y' = -m_1 y,$$

(20)

that $y' = -m_1 y$ on S^1 and that $x^{(16)} > x^{\star\star}$ is not generally satisfied. It means that the fixed point $\underline{E^{(16)}}$ may, depending on the values of parameters involved, lie in $\overline{G^1}$ and the sliding domain S^2 extends in such a case beyond the line $x = x^{\star\star}$.

Qualitative behavior of the above system is characterized by an appropriate Lyapunov function.

Proposition 4. *Let us denote*

$$A_1 = \frac{a_1\lambda_2 + a_2\lambda_1}{\lambda_1 + \lambda_2}, \qquad L_1 = \frac{\lambda_1\lambda_2}{\lambda_1 + \lambda_2}$$

$$N_1 = \frac{e_1\lambda_1 m_2 + e_2\lambda_2 m_1}{e_1\lambda_1 + e_2\lambda_2}, \qquad E_1 = \frac{e_1\lambda_1 e_2\lambda_2}{e_1\lambda_1 + e_2\lambda_2} \tag{21}$$

and let us consider functions

$$V_2(x, y) = e_1\lambda_1 x - m_1 - m_1 \ln\left(\frac{e_1\lambda_1 x}{m_1}\right) + \lambda_1 y - a_1 - a_1 \ln\left(\frac{\lambda_1 y}{a_1}\right),$$

$$V_3(x, y) = E_1 x - N_1 - N_1 \ln\left(\frac{E_1 x}{N_1}\right) + L_1 y - A_1 - A_1 \ln\left(\frac{L_1 y}{A_1}\right),$$

$$P(x) = V_3(x, y^\star) - V_2(x, y^\star).$$

Then the function $V(x, y)$,

$$V(x, y) := \begin{cases} V_2(x, y) + P(x) & \text{if } y \leqq y^\star \\ V_3(x, y) & \text{if } y > y^\star \end{cases} \tag{22}$$

is a Lyapunov function for system (13) on $\mathbf{R}_+^2 \setminus G^1$, and the set $\omega^+(\mathbf{R}_+^2)$,

$$\omega^+(\mathbf{R}_+^2) = \begin{cases} \{(x, y) \mid V_3(x, y) \leqq \min\{V_3(x^\star, y^{(17)}), V_3(x^{(17)}, y^\star)\}\} \\ \quad \subset G^3 \cup (x^\star, y^{(17)}) \cup (x^{(17)}, y^\star) \quad \text{for } m_1 > m_2 \\ \{(x, y) \mid V_3(x, y) \leqq \min\{V_3(x^{\star\star}, y^{(17)}), V_3(x^{(17)}, y^\star)\}\} \\ \quad \subset G^3 \cup (x^{\star\star}, y^{(17)}) \cup (x^{(17)}, y^\star) \quad \text{for } m_1 < m_2 \\ \{(x, y) \mid V_3(x, y) \leqq V_3(x^{(17)}, y^\star)\} \subset G^3 \cup (x^{(17)}, y^\star) \\ \quad \text{for } m_1 = m_2, \end{cases}$$

is the global attractor for the system (13), see Fig. 3.

Remark. Many biological aspects of the dynamics were discussed in [10]. Here we note that the resulting dynamics strongly resembles that one obtained in the predator–prey model with an alternative food (see Figs. 2 and 3). As in the latter case, the global attractor $\omega^+(\mathbf{R}_+^2)$ consists of neutrally stable Lotka–Volterra trajectories and the dimensionality of the problem ($n = 2$) again implies that trajectories cannot enter the interior of the attractor from outside and for all $x_0 \notin \omega^+(\mathbf{R}_+^2)$ thus holds:

$$\omega^+(x_0) = \partial(\omega^+(\mathbf{R}_+^2))$$

$$= \begin{cases} \{(x, y) \mid V_3(x, y) = \min(V_3(x^\star, y^{(17)}), V_3(x^{(17)}, y^\star))\} & \text{for } m_1 \neq m_2 \\ \{(x, y) \mid V_3(x, y) = V_3(x^{(17)}, y^\star)\} & \text{for } m_1 = m_2. \end{cases}$$

The solutions with initial conditions outside the global attractor again exhibit a finite transient period after which they enter a limit Lotka–Volterra cycle that constitutes the border of the global attractor. After the transient period, both prey and predators are permanently distributed in both patches (although in a time-fluctuating ratio), that is the limiting strategy of both populations is always mixed, and the switching again leads to persistence and partial stabilization of the system.

6. Conclusion and remarks

In this paper we showed how Lyapunov functions for differential inclusions can be used to describe global behavior of "piecewise" Lotka–Volterra differential inclusions. Such equations are obtained when we apply principles of optimal foraging theory in population dynamics. We considered two basic types of models: prey and patch models. In both cases it was shown [9–11] that adaptive foraging behavior enhances permanence of the system. Moreover, the resulting Lotka–Volterra differential inclusions behave qualitatively different from the classical Lotka–Volterra differential equations, for which the trajectories are closed curves centered around the equilibrium (and no bounded attractor exists). The effect of optimal foraging typically reduces the amplitude of such oscillations, i.e., it leads to "partial stabilization" of the system.

The reduction of the oscillation amplitude is given by the emergence of the global bounded attractor which consists of neutrally stable Lotka–Volterra cycles centered around an equilibrium point in all studied cases. If the initial conditions lie in the respective attractor, then the system follows usual Lotka–Volterra dynamics with a periodic trajectory. If the initial conditions lie outside the attractor, then the trajectory either enters the attractor in a finite time or approaches the attractor from outside.

Obviously, the loss of the neutral stability of the original Lotka–Volterra system and its change to a globally stable dynamics can be achieved by other alterations of the original system, such as adding density dependent terms for the prey. However, it should be emphasized that the inclusion of optimal individual behavior in the system can give rise to a qualitatively new behavior, such as the appearance of alternative equilibria in the sliding mode. This is the case of the two-patch model considered in Section 4; there are no non-trivial equilibria in the corresponding model with predators behaving at random (i.e., with the controls u_i fixed), and the system is then not

persistent as one of the prey populations always dies out [10]. In a host-parasitoid system examined in [17], the optimal adaptive behavior was also shown to stabilize an otherwise unstable and non-persistent dynamics for a range of parameter values, again giving rise to a locally stable equilibrium in the sliding mode.

This contrasts strikingly with a statement in [3], where the authors claim that "in a continuous-time framework, when migration is fast, optimal migration decisions by predators have little influence on the stability of predator–prey systems". It is also stated in [3] that "In Krivan's (1997) framework, … differences in predator mortality between patches play an important role on persistence of this model (i.e., model presented in Section 4): when predator mortalities do not differ, persistence is still possible but under much restricted conditions." As we proved in this paper (see also [5], [10]), the latter statement is obviously incorrect: the existence of a global attractor and persistence of the system is not qualitatively affected by the predator mortality rates.

The biological phenomena arising from our models agree well with intuitive assessment of the respective models which can be summed up in the phrase "if there is a good place, go there; if there is a good prey, take it". In the case of the predator–prey model with an alternative food, the predator ultimately becomes either generalist (Fig. 2B), feeding on both prey types if the alternative food is "high-valued", or specialist (Fig. 2A), avoiding the alternative food if the latter is "low-valued". In the two patch model where only predators are free to move, predator population ultimately uses both resources and splits (and permanently partly moves) among both prey patches. Finally, in the two patch model with both predators and prey moving between patches, both populations occupy both niches (Fig. 3), again in a time-fluctuating ratio.

7. Appendix

7.1. *Proof of Proposition 1*

The proof is a variant of known proofs for ordinary differential equations with continuous right-hand side; we utilize the relation $\dot{V}(x) \leqq \dot{V}^{\star}(x)$. See, e.g., [16] for details. $\qquad\square$

7.2. Proof of Corollary 1

The properties of V ensure that the compact set $\overline{\omega^+(\mathbf{R}^n_+)}$ is stable and attracts all points in G. Moreover $\xi_{x_0}(t) \to \overline{\omega^+(\mathbf{R}^n_+)}$ for all $x_0 \in \mathbf{R}^n_+$ follows from the repelling condition. $\qquad\qquad\qquad\square$

7.3. Proof of Proposition 2

It suffices to show that conditions of Proposition 1 and Corollary 1 are satisfied.

If $mh_2 > e_2$, then

$$\langle \nabla V_2(x_1, x_3), f^1(x_1, x_3) \rangle = \frac{\lambda_2 K}{1 + h_2 \lambda_2 K} (a_1(e_1 \lambda_1 h_2 x_1 - e_2)$$
$$+ (e_2 - mh_2)\lambda_1 x_3) < 0$$

for $(x_1, x_3) \in G^1$,

$$\langle \nabla V_2(x_1, x_3), f^2(x_1, x_3) \rangle = 0 \quad \text{for } (x_1, x_3) \in G^2,$$

$$\sup_{0 \leqq \alpha \leqq 1} \langle \nabla V_2(x_1, x_3), \alpha f^1(x_1, x_3) + (1 - \alpha) f^2(x_1, x_3) \rangle = 0$$

for $(x_1, x_3) \in M$.

It follows that $\dot{V}^\star(x) \leqq 0$ for all $x \in \mathbf{R}^2_+$ and that $\Lambda = G^2 \cup M$. We conclude that the largest positively invariant subset of Λ is the set $\{(x_1, x_3) \in \Lambda | V_2(x_1, x_3) \leqq V_2(x_1^\star, q^2)\}$. Due to the sliding mode behavior (see Fig. 2A) and the neutral stability of Lotka–Volterra cycles in G^2, the set

$$\omega^+(\mathbf{R}^2_+) = \{(x_1, x_3) | V_2(x_1, x_3) \leqq V_2(x_1^\star, q^2)\} \subset G^2 \cup (x_1^\star, q^1).$$

Finally $\omega^+(\mathbf{R}^2_+)$ is closed which completes the proof.

If $mh_2 < e_2 < mh_2 + m/(\lambda_2 K)$, then

$$\langle \nabla V_1(x_1, x_3), f^1(x_1, x_3) \rangle = 0 \quad \text{for } (x_1, x_3) \in G^1,$$

$$\langle \nabla V_1(x_1, x_3), f^2(x_1, x_3) \rangle = - \frac{\lambda_2 K}{1 + h_2 \lambda_2 K} (a_1(e_1 \lambda_1 h_2 x_1 - e_2)$$
$$+ (e_2 - mh_2)\lambda_1 x_3) < 0$$

for $(x_1, x_3) \in G^2$,

$$\sup_{0 \leqq \alpha \leqq 1} \langle \nabla V_1(x_1, x_3), \alpha f^1(x_1, x_3) + (1 - \alpha) f^2(x_1, x_3) \rangle = 0$$

for $(x_1, x_3) \in M$,

and the reasoning is completed similarly as in the case of $mh_2 > e_2$.

Finally if $mh_2 = e_2$, then

$$\langle \nabla(V_1 + V_2)(x_1, x_3), f^1(x_1, x_3) \rangle = \frac{\lambda_2 K a_1}{1 + h_2 \lambda_2 K}(e_1 \lambda_1 h_2 x_1 - e_2) < 0$$

for $(x_1, x_3) \in G^1$,

$$\langle \nabla(V_1 + V_2)(x_1, x_3), f^2(x_1, x_3) \rangle = -\frac{\lambda_2 K a_1}{1 + h_2 \lambda_2 K}(e_1 \lambda_1 h_2 x_1 - e_2) < 0$$

for $(x_1, x_3) \in G^2$,

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla(V_1 + V_2)(x_1, x_3), \alpha f^1(x_1, x_3) + (1 - \alpha) f^2(x_1, x_3) \rangle = 0$$

for $(x_1, x_3) \in M$;

thus $\Lambda = M$. As $M \backslash S$ are points of transversal motion and S consists of fixed points, we get the results. $\qquad \square$

7.4. Proof of Proposition 3

It holds that

$$\langle \nabla V(x), f^1(x) \rangle = a_2 \lambda_1 (m_1 - m_2 - x_1 + x_2) < 0 \quad \text{for } x \in G^1$$

$$\langle \nabla V(x), f^2(x) \rangle = a_1 \lambda_2 (x_1 - x_2 + m_2 - m_1) < 0 \quad \text{for } x \in G^2.$$

Moreover, $\langle \nabla V(x), \eta \rangle = 0$ for all $\eta \in K(x)$ and $x \in M$, which implies $\Lambda = M$ and the proof is then completed in the same way as in the case of Proposition 2. $\qquad \square$

7.5. Proof of Proposition 4

It suffices to verify the conditions of Proposition 1 and Corollary 1. As G^1 is repelling, we take $G = \mathscr{S}^+(G) = \mathbf{R}_+^2 \backslash G^1$; obviously the conditions (i)–(iii) of Proposition (1) are satisfied and the function $V(x, y)$ is non-negative, with min $V(x, y) = 0$ at $E^{(17)}$. Moreover it is easy to see that $V(x, y) \in C^1(\mathbf{R}_+^2)$, and thus locally lipschitz and regular in $\mathscr{S}^+(G)$. First we consider the case $m_1 \neq m_2$. If $m_1 > m_2$, it holds that

$$\langle \nabla V(x, y), f^3(x, y) \rangle = 0 \quad \text{for } (x, y) \in G^3$$

$$\langle \nabla V(x, y), f^2(x, y) \rangle = \frac{e_1 \lambda_1}{e_1 \lambda_1 + e_2 \lambda_2}(e_1 \lambda_1 x - m_1 + m_2)(\lambda_1 y - a_1)$$

$$< 0 \quad \text{for } (x, y) \in G^2,$$

and on the discontinuity manifolds M^1 and M^2:

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^1(x, y) + (1 - \alpha) f^2(x, y) \rangle = 0$$

for $(x, y) \in M^1$, $y < y^\star$,

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^1(x, y) + (1 - \alpha) f^3(x, y) \rangle = 0$$

for $(x, y) \in M^1$, $y > y^\star$,

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^2(x, y) + (1 - \alpha) f^3(x, y) \rangle = 0$$

for $(x, y) \in M^2$.

It follows that $\Lambda = G^3 \cup M^1 \cup M^2$. It is then easy to verify that the largest positively invariant subset of Λ is $\overline{G^3}$ except the graph of trajectories that cross M^2 with $x < x^{(16)}$, and the attractor is the set

$$\mathscr{A} = \{(x, y) \,|\, V_3(x, y) \leq \min\{V_3(x^\star, y^{(17)}), V_3(x^{(17)}, y^\star)\}\}$$
$$\subset G^3 \cup (x^\star, y^{(17)}) \cup (x^{(17)}, y^\star).$$

If $m_1 < m_2$ then the preceding holds except that on the manifolds:

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^1(x, y) + (1 - \alpha) f^3(x, y) \rangle = 0$$

for $(x, y) \in M^1$,

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^1(x, y) + (1 - \alpha) f^2(x, y) \rangle =$$

$$- \frac{e_1 \lambda_1 a_2}{e_1 \lambda_1 + e_2 \lambda_2} (e_1 \lambda_1 x - m_1 + m_2) < 0$$

for $(x, y) \in M^2$, $x < x^{\star\star}$,

$$\sup_{0 \leq \alpha \leq 1} \langle \nabla V(x, y), \alpha f^2(x, y) + (1 - \alpha) f^3(x, y) \rangle = 0$$

for $(x, y) \in M^2$, $x > x^{\star\star}$.

Finally, using the same procedure and taking in mind that $G^1 = M^1 = \emptyset$ for $m_1 = m_2$, we get the results. □

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