

Selective strategies in food webs

RINALDO M. COLOMBO

Mathematical Department, University of Milan, Via Saldini 50, 20133 Milano, Italy

VLASTIMIL KŘIVAN

Biological Research Center, Academy of Sciences of the Czech Republic,
Branišovská 31, 370 05 České Budějovice, Czech Republic

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Food webs are described as control systems where the controls are chosen according to given myopic strategies. In particular, strategies describing selective feeding and selective escape are defined. The existence of optimal myopic solutions and their uniqueness are discussed. Computer simulations modelling 'switching' are given for a one-predator–two-prey system.

Keywords: population dynamics; food web; control system; selective predation; switching.

1. Introduction

Since the time of Lotka and Volterra, interactions among populations and more generally evolution of ecological systems have been modelled by differential or difference equations. Since various *strategies* may influence the interactions among different populations and thus the fate of the whole system, complex systems cannot be described by coupling many one-prey–one-predator differential equations. These strategies are both internal (e.g. due to *selective feeding*) and external (e.g. due to interactions of the environment with the system). In the literature, man-made strategies (i.e. controls) were considered especially in connection with the management of renewable resources (see Clark, 1976). Internal strategies were studied in connection with *switching* (Legovic, 1989; Murdoch *et al.*, 1975; Oaten & Murdoch, 1975; Pulliam, 1981; Roughgarden, 1979). Several factors may determine feeding preferences for predators. For example, in the case of *Acanthaster planci* feeding on different coral species (Moran, 1986), these factors comprise abundance of corals, accessibility of corals, nutritional value of corals, etc. In general, it is often believed that predators forage so as to maximize their short-term rate of resource intake.

In this paper we consider systems of interacting populations, each of which may utilize several resources and at the same time be a resource for others. Therefore different populations may adopt different strategies. The main questions are: what is a strategy and which strategies will be adopted? Or, in other words, according to which criteria should be strategies be chosen? It seems reasonable to postulate that any population optimizes some given quantity. This leads us to adopt the following procedure. We assume that the various populations choose strategies so that some given quantities are optimized at *any time*. In other words, at *any instant* the system

is in an *optimal* situation. We call these strategies *myopic*, stressing the absence of any insight in the future. This approach is particularly suitable whenever the controllers cannot predict the future, their goal thus being to achieve immediate optimal results.

We stress here that, contrary to the framework above, in the traditional case of intertemporal optimization, controls are driven on the basis of predictions of the future and reach optimality on a whole time interval. This is hardly acceptable when the controls are not driven by human beings.

The strategies above lead to differential inclusions with upper semicontinuous right-hand sides allowing us to model switching. Under reasonable assumptions, these strategies lead to problems that admit a solution. Trying to keep mathematical difficulties to a minimum, we show the main features of these strategies.

The next section defines the mathematical model, i.e. the trophic levels, the equations, and the strategies. Section 3 develops the concept of *strategy*, while Section 4 deals with switching in predation. A short discussion of the results is presented in Section 5.

2. Mathematical model

Let us consider an ecosystem consisting of n populations. This section is devoted to the mathematical formalization of the *structure*, the *dynamics*, and the *strategy* of the system.

The *structure* of the ecosystem is described by a set-valued map $\varphi: \{1, \dots, n\} \rightsquigarrow \{1, \dots, n\}$, called the *food web map*. This map associates to each index j in $\{1, \dots, n\}$ the set of the indices of those populations on which the j th population may feed. For example, $\varphi(j)$ is empty whenever the j th population does not feed on any other population. We call the food web map *monotone* if

$$i \in \varphi(j) \Rightarrow i < j, \quad (2.1)$$

Provided that the numbering of the populations is well chosen, this property is shared by those ecosystems that contain no cycles. Under (2.1), trophic levels may be recursively characterized by φ : if L_r denotes the r th trophic level, then

$$\begin{aligned} L_1 &= \{i \in \{1, \dots, n\} : \varphi(i) = \emptyset\}, \\ L_r &= \left\{ i \in \{1, \dots, n\} : \varphi(i) \subseteq \bigcup_{l=1}^{r-1} L_l \right\} \quad \text{for } r > 1. \end{aligned}$$

The *dynamics* of the ecosystem is given by the following control system (see also Krivan, 1991):

$$\dot{x}(t) = f(t, x(t), u(t)), \quad u(t) \in \mathcal{U}, \quad (2.2)$$

where

$x(t) = (x_1(t), \dots, x_n(t))$ is the vector quantifying the populations;

$f(t, x, u) = g(t, x, u) - h(t, x, u)$ is the (n -dimensional) growth function, where $g(t, x, u)$ is the natality function and $h(t, x, u)$ is the mortality function;

$\mathcal{U}$ is the compact convex set of the admissible values for the controls u .

More precisely, we consider natality and mortality functions of the following forms:

$$\begin{aligned} g_i(t, x, u) &= a_i(t, x) + \sum_{j \in \phi(i)} s_{ji}(t, u) b_{ji}(t, x_j) x_i \\ h_i(t, x, u) &= c_i(t, x) + \sum_{j \in \phi^{-1}(i)} s_{ij}(t, u) k_{ij} b_{ij}(t, x_i) x_j \end{aligned} \quad (i = 1, \dots, n). \quad (2.3)$$

Here a_i and c_i are the *intrinsic* natality and mortality functions respectively; b_{ij} (also called the *trophic function*) denotes the natality rate of the j th population due to its feeding only on the i th population. All the a_i , b_{ij} , and c_i are defined on $\mathbb{R}_+ \times \mathbb{R}_+^n$, where $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_1 \geq 0, \dots, x_n \geq 0\}$ is the positive octant. To ensure the invariance of $\mathbb{R}_+^n$ with respect to (2.2), we require

$$\begin{aligned} a_i(t, 0) &= 0 \quad \text{and} \quad c_i(t, 0) = 0 \quad \text{for any } i = 1, \dots, n, \\ b_{ij}(t, 0) &= 0 \quad \text{for any } i, j = 1, \dots, n. \end{aligned} \quad (2.4)$$

The $s_{ij}(t, u)$ are defined on $\mathbb{R}_+ \times \mathcal{U}$ and model how the components of u are *superposed* (i.e. combined) at time t to control the interaction between the j th and the i th populations. We will assume that s_{ij} is linear in the control. Finally, the k_{ij} are the given *efficiency coefficients*. All the functions introduced so far are assumed to be continuous and nonnegative wherever they are defined.

A *myopic strategy* is a set-valued map $S: \mathbb{R}_+ \times \mathbb{R}_+^n \rightsquigarrow \mathcal{U}$, i.e. S associates to any (t, x) a subset $S(t, x)$ of $\mathcal{U}$. In other words, it is a rule to select among the admissible controls. Hence, the actual behaviour of the system is described by the solutions of

$$\dot{x}(t) = f(t, x(t), u(t)), \quad u(t) \in S(t, x(t)), \quad x(t_0) = x_0, \quad (2.5)$$

where $(t_0, x_0) \in \mathbb{R}_+ \times \mathbb{R}_+^n$ is some given initial condition.

A result assuring the existence of at least one solution of (2.5) is given in Appendix A (see Proposition 1). This theorem says that in our setting (2.5) has always at least one solution, provided that the graph of the myopic strategy maps is a closed set. Let us stress that without assuming the linearity of the maps s_{ij} in u , (2.5) may have no solutions at all.

Many different controls may influence the interactions among populations. These controls may be both *internal* and *external*. Assume that m controllers regulate the system and that $\mathcal{U} = \mathcal{U}^1 \times \dots \times \mathcal{U}^m$, with $\mathcal{U}^l$ the convex compact set in which the controls driven by the l th controller may vary.

In what follows we will consider myopic strategies defined through optimality conditions of the form

$$S(t, x) = \left\{ u \in \mathcal{U} : d^l(t, x, u^l) = \min_{v \in \mathcal{U}^l} d^l(t, x, v) \text{ for } l = 1, \dots, m \right\}, \quad (2.6)$$

where $d^l: \mathbb{R}_+ \times \mathbb{R}_+^n \times \mathcal{U}^l \rightarrow \mathbb{R}$ is a continuous *cost function* to be minimized at any instant by the l th controller.

As we saw, in order to have a solution of (2.5), the graph of the strategy map $S(t, x)$ must be closed. For $S(t, x)$ defined by (2.6), this is true if all $d^l(t, x, u)$ are convex in u (see Appendix A, Proposition 2). We stress that d^l is not required to be linear in u^l .

In the case where the system must satisfy further constraints of the kind $x(t) \in K$ for some closed $K \subseteq \mathbb{R}_+^n$, viability theory (Aubin, 1992) gives conditions ensuring the existence of solutions of (2.5) subjected to this constraint. These conditions amount to adding to the assumptions of Proposition 1 that the map

$$R: \mathbb{R}_+ \times K \rightsquigarrow \mathcal{U}: (t, x) \mapsto \{u \in \mathcal{U}: f(t, x, u) \in T_K(x)\}$$

be lower semicontinuous with convex compact values and $R \cap S$ be never empty (Aubin, 1992). Here $T_K(x)$ is the contingent cone (see Aubin & Cellina, 1984: p. 176, Def. 1).

In general, (2.5) may have no global solutions, i.e. solutions defined on $[0, \infty)$. In fact, the growth of some population may be so fast as to *blow up*, i.e. to reach infinity in a finite time. However, this is not possible when the food web map is monotone and the intrinsic natality functions have linear growth, i.e. $a_i(t, x) \leq A_i(1 + x_i)$ for some $A_i > 0$ (see Appendix A, Proposition 3).

In general, (2.5) may have more solutions. Moreover, to a given evolution $x(t)$ there may correspond more than one control function u . In this case methods based on probability theory, metric likelihood (Cellina & Colombo, 1990), or fuzzy likelihood (Colombo & Křivan, 1992) may allow us to estimate how much a prediction of the behaviour of the system is reliable. Nevertheless, in many cases, despite the multivalued character of the right-hand side of (2.5), right uniqueness (i.e. uniqueness in the future) for its solutions may still hold. See Appendix B for a discussion on the mathematical hypotheses implying right uniqueness.

3. Selective feeding and selective escape

In this paper we consider systems driven by *internal* controllers. Let us note that system (2.5) together with (2.6) provides a framework which is general enough to describe not only selective feeding but also *selective escape* and many other controllers that may arise. Within this framework we may even consider different controllers for different populations, for example selective escape for prey and selective feeding for predators. Indeed, consider $u^i = (p^i, e^i)$, where p^i is a vector of parameters controlling the predation of the i th population, i.e. it models selective feeding. The vector e^i is a vector whose j th component p_j^i expresses how much the i th population tries to feed on the j th prey. Analogously, e_j^i is the j th component of e^i which expresses how much the i th population tries to escape from the j th predator. We should stress here that $e_j^i = 0$ means maximal escape of the i th population from the j th predator while $e_j^i = 1$ means no escape at all. Therefore

$$\mathcal{U}^i = \mathcal{P}^i \times \mathcal{E}^i,$$

where

$$\mathcal{P}^i = \left\{ p^i \in [0, 1]^n: p_j^i = 0 \text{ if } j \notin \varphi(i); \sum_{j \in \varphi(i)} p_j^i = 1 \text{ if } \varphi(i) \neq \emptyset; i, j = 1, \dots, n \right\}$$

$$\mathcal{E}^i = \left\{ e^i \in [0, 1]^n: e_j^i = 0 \text{ if } j \notin \varphi^{-1}(i); \sum_{j \in \varphi^{-1}(i)} e_j^i = 1 \text{ if } \varphi^{-1}(i) \neq \emptyset; i, j = 1, \dots, n \right\}$$

defines the set of the admissible controls.

The functions s_{ij} may take different forms; for example

$$s_{ij}(t, u) = \beta_{ij}(t)p_i^j + \gamma_{ij}(t)e_j^i, \quad (3.1)$$

β_{ij} and γ_{ij} being nonnegative continuous functions on $\mathbb{R}_+$. Note that this assumption implies the independence of the effects of the choices of a population from the choices of the other populations. Formula (3.1) may be interpreted in two ways:

- the superposition of the choices of the predators and of the prey is given by a weighted average of their control parameters;
- a first-order approximation of more general and complex functions s_{ij} is considered.

Let us note that in the particular case $\beta_{ij} \neq 0$ and $\gamma_{ij} = 0$ we recover the selective feeding.

A different choice of s_{ij} , like for example $s_{ij}(t, u) = \eta_{ij}(t)p_i^j e_j^i$, has totally different consequences; in this case the feeding may take place only if *both* the prey *and* the predator want it, which is hardly acceptable.

4. Switching during predation

The most studied case in literature is switching when a predator feeds on two or more prey choosing the 'most convenient' one at each instant. The 'most convenient' may have different meanings; for example it may be synonymous with the most abundant or the most nutritional, etc. Depending on this meaning, we may define different strategies. Here we will consider only two of them: *maximum growth strategy* and *maximum density strategy*. Some other strategies may be treated in an analogous way.

First, we consider the maximum growth strategy, which is: *each predator maximizes its own growth*. In other words, we model the problem of selective feeding as an optimization problem, the quantities to be optimized being the growth functions of the populations. Moreover, we assume that the populations' behaviour is *noncooperative*, i.e. any population maximizes its own growth, independently of the others' choices. Then the set of controls that correspond to this strategy is

$$S_M(t, x) = \left\{ p \in \mathcal{P} : f_i(t, x, p) = \max_{\{v \in \mathcal{P} : v^j = p^j, j \neq i\}} f_i(t, x, v) \text{ for } i = 1, \dots, n \right\}.$$

Note that the maximum of f_i is taken, varying only that part of v which depends on the i th population. Notice that $S_M(t, x)$ is the set of points of Nash maxima of f over $\mathcal{P}$ for fixed (t, x) (Aubin & Ekeland, 1984).

This strategy is obtained when we set $d^i(t, x, p^i) = -f_i(t, x, p^i)$. Hence, the existence of maximal growth solutions follows from Appendix A (Proposition 2).

Another possible strategy, which we call the *maximal density strategy*, is the one in which *predators feed on the most abundant prey*. This leads to the following n cost functions:

$$d^i(t, x, p^i) = - \sum_{j \in \varphi(i)} x_j p_j^i.$$

Example. Assume there are three populations whose interaction structure is described by $\varphi(1) = \emptyset$, $\varphi(2) = \emptyset$, and $\varphi(3) = \{1, 2\}$; hence $L_1 = \{1, 2\}$ and $L_2 = \{3\}$. The dynamics of the interaction among the populations and the feeding strategy are described by

$$\begin{cases} \dot{x}_1 = a_1 x_1 - b_{13} p_1^3 x_1 x_3, \\ \dot{x}_2 = a_2 x_2 - b_{23} p_2^3 x_2 x_3, \\ \dot{x}_3 = k_{13} b_{13} p_1^3 x_1 x_3 + k_{23} b_{23} p_2^3 x_2 x_3 - c_3 x_3, \\ p \in S_M(x). \end{cases} \quad (4.1)$$

In this example, the only controller is the predator. Assume that $a_1 < a_2$; then we say that the first population is *weaker* than the second.

A portrait of the evolution of the system may be obtained through a simple qualitative reasoning. Assume $x_1(t_0) \neq 0$, $x_2(t_0) \neq 0$, and $x_3(t_0) \neq 0$; then the orbit starting from $x(t_0)$ eventually enters in $\{x \in \mathbb{R}_+^3 : k_{13} b_{13} x_1 = k_{23} b_{23} x_2\}$. More precisely, it remains there always unless $x(t)$ reaches the critical region defined by

$$x_3 \leq (a_2 - a_1)/b_{23}, \quad (4.2)$$

and in this case the orbit enters the region

$$\{x \in \mathbb{R}_+^3 : k_{13} b_{13} x_1 < k_{23} b_{23} x_2\},$$

since we assumed $a_2 > a_1$ (see Appendix B).

From the biological point of view, this may be interpreted as follows. The predator feeds on the 'most convenient' prey, if possible. Otherwise, if neither of the two prey is more convenient than the other, the predator feeds on both prey as long as possible. If its density falls below the critical value (4.2), this balanced situation needs to be abandoned. Hence the predator starts feeding only on the prey with the *highest* natality rate. This choice of the predator allows the weaker prey to increase at its maximum available natality rate, in our case exponentially. After a while, the weaker prey is again as convenient as the stronger one, and a balanced situation is again reached. Note that this *balancing effect* of the predator was not postulated but is a consequence of the proposed strategy.

A picture of this balancing effect is shown in Fig. 2. We see that the system starts in a situation decoupled in two subsystems. The first subsystem consists of x_2 and x_3 and evolves along a cycle of Lotka-Volterra type, while the second one consists of x_1 alone, which grows exponentially. When x_1 is as convenient as x_2 , the cycle breaks down and the growth rate of x_1 is reduced due to the predation by x_3 . After a transient period the system settles into a dynamic equilibrium which moves along a new cycle.

The results of a numerical simulation for this system are shown in Figs. 1 and 2. Advanced numerical methods for the treatment of such equations with more examples are discussed in Kastner-Maresch & Křivan (1993).

5. Conclusion

This paper presents a deterministic model for the evolution of ecosystems with controls, the controllers being members of the ecosystem or outsiders, or both. Controls

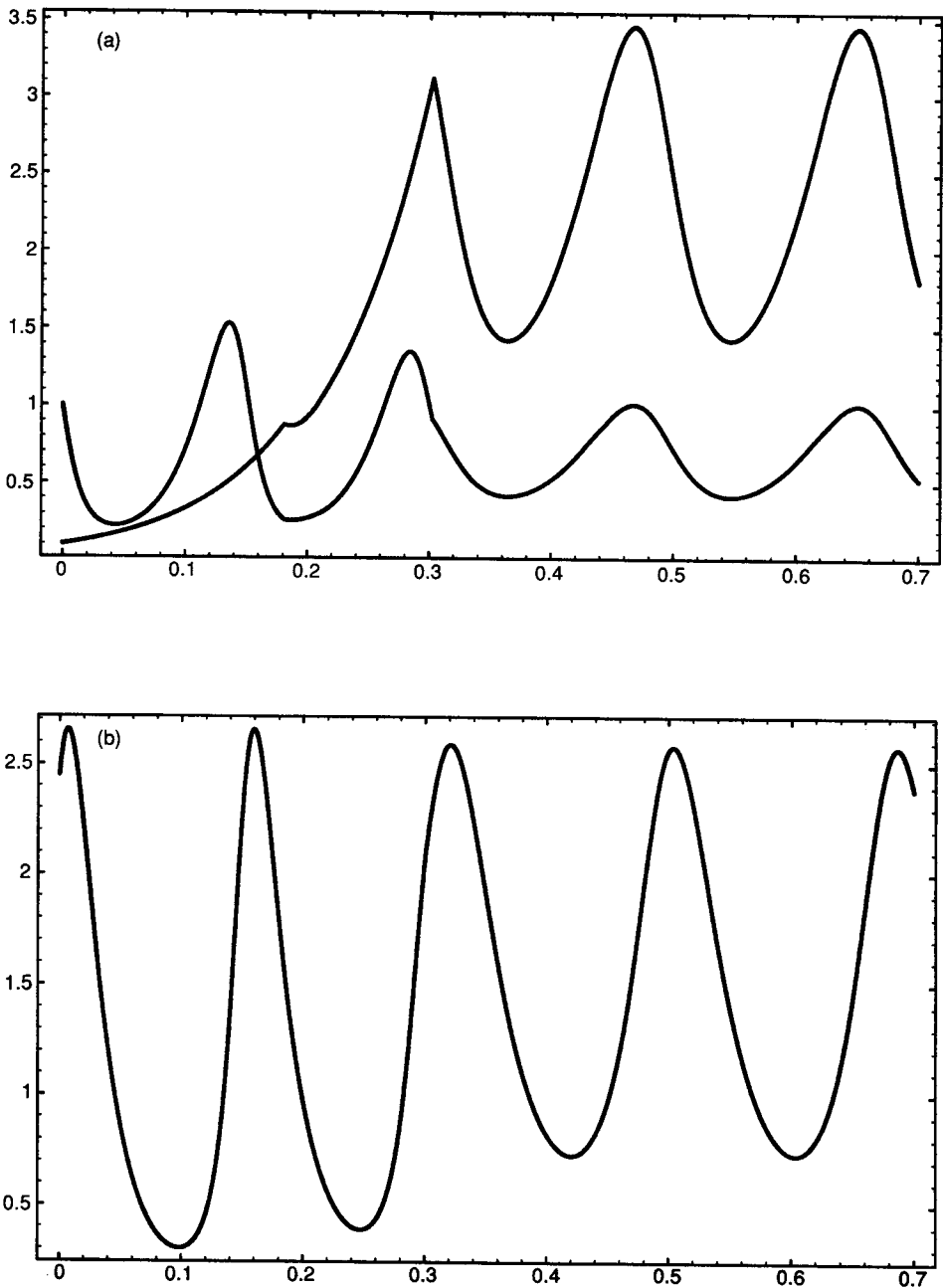


FIG. 1. Computer simulations for system (4.1), using the Runge-Kutta method. The values of the parameters are: $a_1 = 12$; $a_2 = 40$; $b_{13} = 31$; $b_{23} = 37$; $k_{13} = 0.7$; $k_{23} = 2$; $c_3 = 50$; $x_1(0) = 0.1$; $x_2(0) = 1$; $x_3(0) = 2.45$. In (a) the densities of the prey (x_1, x_2) are plotted as functions of time, while in (b) it is the density of the predator (x_3) that is plotted.

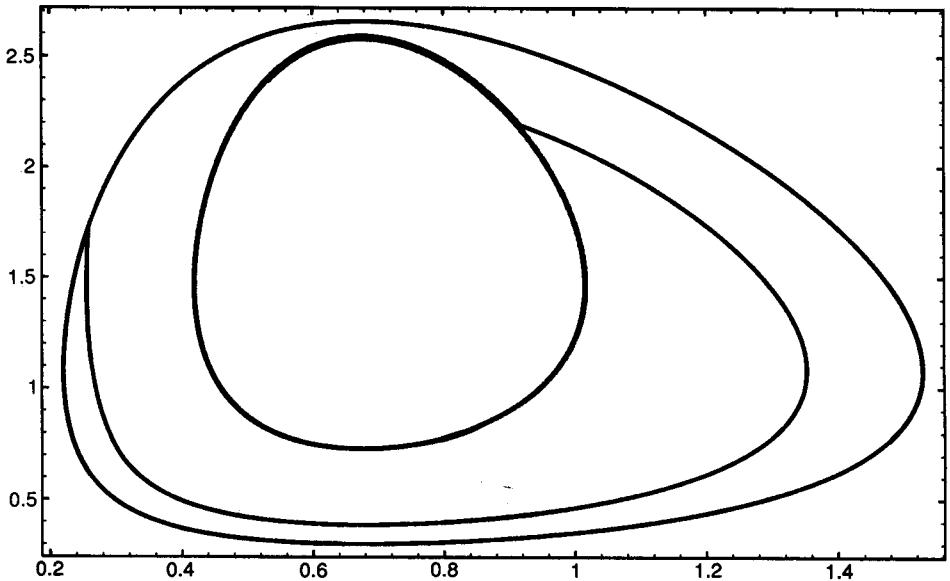


FIG. 2. Phase plot of the simulation from Fig. 1 projected on the (x_2, x_3) plane. The original Lotka–Volterra cycle followed by a transient trajectory and the new cycle arising from switching are clear in this plot.

are chosen according to *myopic* strategies. Such an approach seems particularly suitable in the case where the controllers do not (or cannot) forecast the future development of the system. The model presented in this paper is general enough to cover complex systems.

This model could also be used to postulate and verify different strategies for different systems. For example, taking the system described in the Example, we could estimate all parameters from one-prey–one-predator experiments. Comparing the results obtained from simulations for a particular strategy with the real data would allow us to infer the typical strategies for given populations. There may be some obstacles when applying this approach to real populations, caused for example by delay in switching and by stochastic effects (especially for small populations). Both these phenomena may be included in our model. However, this would increase the mathematical difficulties without affecting the basic properties of our approach.

The effects of switching seem to be particularly relevant during transitory situations like the entering of a new population in a system. In the long run, switching leads to dynamic equilibria not easily distinguishable from what is foreseen by the traditional Lotka–Volterra models. Let us note that switching seems to produce oscillations in the densities of populations rather than stabilizing the dynamics in an equilibrium as is generally assumed.

Appendix A

PROPOSITION 1 With the assumptions stated in the paper, if the strategy S has a closed graph and nonempty convex values, then for any initial condition $(t_0, x_0) \in$

$\mathbb{R}_+ \times \mathbb{R}_+^n$ there exist a (strictly) positive T , an absolutely continuous $x: [t_0, t_0 + T] \mapsto \mathbb{R}_+^n$, and a bounded measurable $u: [t_0, t_0 + T] \mapsto \mathcal{U}$ that satisfy (2.5).

Proof. Corollary 1 on p. 42 of Aubin & Cellina (1984) ensures that S is upper semicontinuous. Due to Proposition 1 on p. 41 of the same book, the map $F_S(t, x) = f(t, x, S(t, x))$ is upper semicontinuous too. Moreover, S has compact convex values and f is continuous and linear in the third argument; hence also F_S has compact convex values. Corollary 1 on p. 129 ensures that the Cauchy problem

$$\dot{x}(t) \in F_S(t, x(t)), \quad x(t_0) = x_0$$

admits an absolutely continuous solution x on an interval $[t_0, t_0 + T]$. Moreover, (2.4) ensures that $x(t) \in \mathbb{R}_+^n$ for all t . Following Corollary 1 on p. 91 of Aubin & Cellina (1984), one may prove the existence of a measurable $u: [t_0, t_0 + T] \mapsto \mathcal{U}$ such that the pair (x, u) is a solution to (2.5). $\square$

PROPOSITION 2 If the internal strategy S is given by (2.6) and the d^i ($i = 1, \dots, m$) are convex in the third variable, then S satisfies the assumptions of Proposition 1.

Proof. The nonemptiness of $S(t, x)$ is straightforward. Theorem 5 on p. 25, Theorem 1 on p. 41, and Proposition 2 on p. 41 of Aubin & Cellina (1984) imply the closedness of the graph. The convexity of d^i in u^i implies the convexity of $S(t, x)$. $\square$

PROPOSITION 3 Let the hypotheses of Proposition 1 hold. Assume, moreover, that φ satisfies (2.1) and any a_i has linear growth, i.e. $a_i(t, x) \leq A_i(t)(1 + x_i)$ where $A_i: [0, \infty) \mapsto \mathbb{R}_+$ is continuous. Then any solution to (2.5) may be extended to $[t_0, \infty)$.

Proof. The proof is by induction on the trophic level. Let i be in L_1 . Then $\dot{x}_i \leq A_i(t)(1 + x_i)$, which ensures the global existence of x_i . Let i be in L_r , with $r > 1$. Then

$$\dot{x}_i \leq A_i(t)(1 + x_i) + \sum_{j \in \varphi(i)} s_{ji}(t, u) b_{ji}(t, x_j(t)) x_i,$$

which, owing to the compactness of $\mathcal{U}$, again ensures the global existence of x_i . $\square$

Appendix B

Right uniqueness for (2.5) follows from the one-sided Lipschitz condition for the map $F_S(t, x) = f(t, x, S(t, x))$; see Theorem 1 on p. 106 of Filippov (1988) or Kastner-Maresch & Křivan (1993). This requirement is not easy to handle in the general situation described by (2.5) and (2.6). However, if there is only one population that may choose between only two possibilities (the case discussed in Section 4, for instance), then right uniqueness is easy to prove.

Consider the myopic strategy map $S: \mathbb{R}_+^n \rightsquigarrow \mathcal{U}$. Let M be the set of those $x \in \mathbb{R}^n$ such that $S(x)$ is not single-valued. Assume that M is a smooth manifold that splits $\mathbb{R}^n$ into two parts that we denote G_1 and G_2 . Let $f_1(t, x)$ denote the unique value of (2.5) for $(t, x) \in G_1$ and similarly for $f_2(t, x)$. For (t, x) such that $x \in M$, $f_1(t, x)$ denotes the limit of f_1 at the point (t, 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 ; $\langle x, y \rangle$ stands for the scalar

product in $\mathbb{R}^n$. The following is Theorem 2 (p. 110) in Filippov (1988), which ensures right uniqueness.

PROPOSITION 4 Let M be a C^2 manifold, and let the vector $f_1(t, x) - f_2(t, x)$ be in C^1 . If for each $t \in \mathbb{R}_+$ 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 right uniqueness for (2.5) holds.

Observe that Proposition 4 implies right uniqueness for (4.1). Indeed, M is given by the equation $k_{13}b_{13}x_1 = k_{23}b_{23}x_2$ and

$$G_1 = \{x \in \mathbb{R}_+^3 : k_{13}b_{13}x_1 > k_{23}b_{23}x_2\}, \quad G_2 = \{x \in \mathbb{R}_+^3 : k_{13}b_{13}x_1 < k_{23}b_{23}x_2\}.$$

A normal vector to M is

$$n = (k_{13}b_{13}/\sqrt{(k_{13}b_{13})^2 + (k_{23}b_{23})^2}, -k_{23}b_{23}/\sqrt{(k_{13}b_{13})^2 + (k_{23}b_{23})^2}, 0).$$

If $\langle f_1(t, x), n \rangle \geq 0$, then

$$\langle f_2(t, x), n \rangle = \langle f_1(t, x), n \rangle + (b_{13}^2 k_{13} x_1 x_3 + k_{23} b_{23}^2 x_2 x_3) / \sqrt{(k_{13}b_{13})^2 + (k_{23}b_{23})^2} > 0.$$

Due to Proposition 4, (4.1) has a unique solution.

Let us note that a solution cannot leave the manifold M if both $\langle f_1(t, x), n \rangle < 0$ and $\langle f_2(t, x), n \rangle > 0$. Since we assumed $a_2 > a_1$, the first inequality is always satisfied, while the second one gives $x_3 > (a_2 - a_1)/b_{23}$. From this we derive the critical region defined by (4.2)

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