An Investigation of the Effect of using Anticipation in a Technological Substitution Model

Mark E. Burke

Department of Mathematics and Statistics, University of Limerick, Limerick, Ireland
Fax: +353 61 334927, Email: mark.burke@ul.ie, http://www.maths.ul.ie/

Abstract. Whether a new technology can successfully compete against an established one, and either hold its own or indeed replace the older technology depends on many factors, not least of which is the ability of the innovators to anticipate how the market and the existing firms will react to the newcomer. In this paper, we describe and contrast the behaviours of a quadratic recurrence relation derived from a \textit{Lotka-Volterra} competition model with that of a similar system which has an anticipatory capability.

Keywords: weak anticipation, technology substitution, two species competitive model, anticipative control

1. INTRODUCTION

The process of technological innovation and subsequent technology substitution has been the subject of much investigation in recent years [10], [21], [22] and [25].

Traditionally mathematical models have been used to describe how a new technology replaces an existing technology in the marketplace. Initially these models expressed how the market share of the new technology grows as a function of its current share and of the potential market available to it, without recourse to the share held by the other technologies present [1], [9], [24]. However these models were soon followed by others which attempt to model the interactions between the technologies. The model-builders have borrowed many ideas from the ecological domain which enable them to see the technologies as interacting species and their growth or decline as interactions of a community of competitors, mutualists or occasionally of predators and prey [2],[14],[15],[18],[19],[20] and [21]. The mainstream approach has been to view the interactions as being purely competitive as the technologies vie for their share of the market. For this reason, chief among the models has been the \textit{Lotka-Volterra} competition equations (LVC) [13],[26].

However, Pistorius and Utterback [18], [19] and [20] argue that rather than just pure competition there may be multi-modal interactions taking place where in addition to competition, sometimes mutualistic behaviours are seen - e.g. when the very existence of the old technology paves the way for the acceptance of the new technology, or the introduction of the new technology gives a fillip to the older one - and sometimes it may be more realistic to view the invading technology as preying on the established technology...at least before the older technology realises it’s being eaten! The converse is also possible of course.

These ideas have also been applied to the problem of an organisation choosing between developing knowledge and skills in-house or buying them in [5], to the analysis of the competition between cellular and PCS technologies in the Korean mobile phone market [12] and to the transition from monochrome to colour in the Japanese TV market [27].

Rather than look at a complex marketplace where there may be many competing technologies or products vying with one other for their share, this paper looks at the scenario where a single invading technology attempts to gain a foothold and potentially displace an established one. It also adopts the viewpoint of the proponents of the new technology who are searching for a successful invading strategy.
1.1 Anticipatory systems

A weak anticipatory system [8] is an anticipatory system [23] which uses predictions of its future behaviour generated by an “internal model” to guide its future actions. This paper uses the particular weak anticipatory paradigm described in [3] and developed in [4] to investigate how invading strategies may be modified and implemented with anticipatory knowledge. In this approach, the anticipatory system consists of a discrete time system S and an internal model M (of S and possibly the environment). The time evolution of S is determined by its current state and input. S sends the state information to M, which off-line generates predictions about the future behaviour of S, and instantaneously returns these predictions to S. S uses this information as an input to determine its own next state.

The structure of the paper is as follows. In section 2, the standard LVC model is introduced and analysed from the viewpoint of how an invading technology can succeed. Some previous work on Anticipatory LVC Systems is reviewed. Section 3 introduces a modified LVC model which, in addition to competition between the technologies, exhibits commensalism whereby the invading technology gains due to the prior existence of the established technology, but the older technology gains nothing from the arrival of the new challenger. The model is compared with the pure competition model and the possible differences in behaviour are identified. In section 4, the modified LVC model is analysed from a management strategy viewpoint and the strategies identified implemented in an anticipatory framework. Section 5 contains a discussion of what the model is capable of and what it cannot show. Many of the ideas used in the paper are natural applications of well known results in mathematical ecology. For convenience, these results are given in the appendices, which review some mathematical aspects of discrete time dynamical models, ecological models of competition and the conditions under which invasion of an environment by a species is possible.

2. THE PURE COMPETITION MODEL

Denoting the size of the established technology at time \( t \) by \( X(t) \) and that of the invading technology by \( Y(t) \), the LVC equations are often presented in the technology growth literature in the form:

\[
\begin{align*}
\frac{dX}{dt} &= R_1 X \left(1 - \frac{X}{K_1} - \alpha_1 \frac{Y}{K_1} \right), \\
\frac{dY}{dt} &= R_2 Y \left(1 - \frac{Y}{K_2} - \alpha_2 \frac{X}{K_2} \right),
\end{align*}
\]

where in ecological terms \( R_1, R_2 \) are the intrinsic growth rates, \( K_1 \) and \( K_2 \) are the carrying capacities and \( \alpha_1 \) and \( \alpha_2 \) are the interspecific competition parameters of the two species (or technologies) respectively. Modis [14] notes that the intrinsic growth rate can be equated with a product’s attractiveness, the carrying capacity with its market niche while the competition or coupling parameter is a measure of how much one technology affects the other. Management strategies should be geared to improve the positioning of the product in the marketplace through manipulation of the above parameters. Modis contends that management actions like performance improvements and price changes can influence a product’s attractiveness while advertising campaigns with an appropriate message at an appropriate time can in principle effect all the parameters of the LVC model - but by how much and at what cost is the question.

Data describing the performance of a technology in terms of quantities of derived products sold are typically collated at discrete points in time. Similarly management decisions are also made at discrete points in time. This suggests using a discrete form of the LVC equations and this is the approach used in this paper. Furthermore in order to facilitate comparison between management strategies, the sizes of the technologies have been normalised to their respective carrying capacities. When an Euler discretisation with a time step “\( h \)” is used, the relationships between the populations at time \( t = kh \) and parameters of (1) and (2) are given by

\[
\begin{align*}
x_k &= \frac{X(kh)}{K_1}, & y_k &= \frac{Y(kh)}{K_2}, \\
r_1 &= R_1 h, & r_2 &= R_2 h, \\
\beta_1 &= \frac{K_2}{K_1} \alpha_1, & \beta_2 &= \frac{K_1}{K_2} \alpha_2.
\end{align*}
\]

where \( x_k \) and \( y_k \) are the normalised sizes of the established and invading technologies, \( r_1 \) and \( r_2 \) are the discretised intrinsic growth rates and \( \beta_1 \) and \( \beta_2 \) the normalised interspecific competition parameters, respectively. The resultant
model or “map”\(^1\) is then
\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k), \\
y_{k+1} &= y_k + r_2 y_k (1 - y_k - \beta_2 x_k).
\end{align*}
\]
(2)

The relative sizes of the \(\beta_i\), \(i = 1, 2\) parameters determine the strength of the interspecific as opposed to the intraspecific competition. When \(\beta_i < 1\), intraspecific competition is structurally greater than interspecific, and when \(\beta_i > 1\), the reverse is true. For the community as a whole, the product \(\beta_1 \beta_2\) determines the character of the interaction, leading to potential co-existence when \(\beta_1 \beta_2 < 1\) or competitive exclusion when \(\beta_1 \beta_2 > 1\), [11].

While nonlinear maps like (2) are capable of chaotic as well as regular behaviours, the choice of intrinsic growth rates used in the following analyses shall focus on behaviours that show equilibria or fixed points, i.e. \(0 < r_i < 2\), \(i = 1, 2\). In addition, in the context of an attempted technology “invasion”, it is reasonable to consider the situation where the existing technology is not overly influenced by the newcomer, i.e. \(\beta_1\) is small \(\approx 0\), but the converse is true for the invader, i.e. \(\beta_2\) is large and \(\beta_1 \beta_2 < 1\).

From Appendices A2 and A3, an invasion can only occur when the existing technology is in stable equilibrium at \(x_k = 1\) and \(\beta_2 < 1\). Thus the fixed point \(\mathbf{x}_2 = (1, 0)\) is an unstable saddle. Coupled with the fact that \(\beta_1 < 1\), this means that the fixed point \(\mathbf{x}_4 = (x^*, y^*)\) given by (21) is positive and stable, and in fact all trajectories converge to it (Fig (1)). On the other hand if \(\beta_2 > 1\), \(\mathbf{x}_2\) is stable and all trajectories converge to it (Fig (2)).

![Figure 1](image)

**FIGURE 1.** LVC model - Invasion: \(r_1 = 1.8, \beta_1 = 0.2, r_2 = 1.5, \beta_2 = 0.9\); (Left) Phase plane and isoclines, (Right) A typical time domain plot of an invasion trajectory

Looking at these results from the viewpoint of an invading strategy, unless the favourable situation of the coupling parameter \(\beta_2 < 1\) occurs naturally, it seems that technological breakthrough may be difficult to achieve without considerable deployment of resources in order to move from a losing parameter value (\(\beta_2 > 1\)) to a successful one (\(\beta_2 < 1\)). The proponents of the new technology need to consider whether advertising alone is sufficient or some other strategies may be required.

In [6], the effect of using a weak anticipatory system by the invader to manage its own growth is investigated. The systems investigated involved either (i) using a prediction of the growth of the established technology alone or (ii) predictions of the growth of both established and invading technologies.

The “internal model” equations (whose variables are distinguished by a tilde), which coincide with the original LVC

\(^1\) Like the logistic map in 1-dimension, this quadratic map is capable of generating negative values of \(x_{k+1}\) or \(y_{k+1}\) for inappropriate choices of the parameters values and/or \(x_k\) and \(y_k\). A discussion of this phenomenon is found in [11] and necessary and sufficient conditions for the ranges of parameter values are given which avoid these biologically infeasible situations. None of the parameter values used in this paper lead to this phenomenon.
FIGURE 2. LVC model - No invasion: \( r_1 = 1.8, \beta_1 = 0.2, r_2 = 1.5, \beta_2 = 1.1 \); (Left) Phase plane and isoclines, (Right) A typical “attempted invasion” time domain plot

model, are

\[
\begin{align*}
\hat{x}_{k+1} &= \hat{x}_k + r_1 \hat{x}_k (1 - \hat{x}_k - \beta_1 \hat{y}_k) \quad (3) \\
\hat{y}_{k+1} &= \hat{y}_k + r_2 \hat{y}_k (1 - \hat{y}_k - \beta_2 \hat{x}_k) \quad (4)
\end{align*}
\]

The output of the internal model feeds into the actual system equations to give: using predictive strategy (i)

\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k) \quad (5) \\
y_{k+1} &= y_k + r_2 y_k (1 - y_k - \beta_2 \hat{x}_{k+1}) \quad (6)
\end{align*}
\]

or using predictive strategy (ii)

\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k) \quad (7) \\
y_{k+1} &= \hat{y}_{k+1} + r_2 \hat{y}_{k+1} (1 - \hat{y}_{k+1} - \beta_2 \hat{x}_{k+1}) \quad (8)
\end{align*}
\]

In both cases it was found that the anticipatory system\(^2\) yielded little or no improvement over conventional management strategies, though the system which used predictions of the future growth of the invader offered more scope for improvement.

3. THE COMPETITION-COMMENSALISM MODEL

Motivated by the observation that multi-modal interactions are possible between competing technologies [20], consider a modified LVC model in which the established technology helps the invader by virtue of, for example, “creating the market”, without any reciprocation by the invader. This commensalism is modelled by an increase in the carrying

\(^2\) In the terminology of [3] and [4], both systems are 1-step weak anticipatory systems. Step here refers to the number of future time steps predicted by the internal model.
capacity of the newcomer from 1 to $1 + cx_k$, [17], where $c$ is a non-negative normalising parameter:

$$
\begin{align*}
    x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k), \\
y_{k+1} &= y_k + r_2 y_k (1 - \frac{y_k}{1 + cx_k} - \beta_2 x_k).
\end{align*}
$$

(9)

From Appendices A2 and A3, the analysis of whether invasion is possible follows along similar lines to the LVC case. Invasion is possible whenever $\beta_2 < 1$. $x_2$ is unstable (19) and $x_4$ is positive and stable. Indeed all trajectories converge to $x_4$ (Fig (3)). On the other hand, when $\beta_2 > 1$, $x_2$ is stable, attracting nearby trajectories; but whenever $c$ satisfies (22)

![Image](image-url)
FIGURE 4. Modified LVC model - High Level Invasion: $r_1 = 1.8$, $\beta_1 = 0.2$, $r_2 = 1.5$, $\beta_2 = 1.1$, $c = 9.0$; (Left) Phase plane, isolines and part of the separatrix, (Right) Typical time domain plots: a failed invasion and a high level success

FIGURE 5. Modified LVC model - No Invasion: $r_1 = 1.8$, $\beta_1 = 0.2$, $r_2 = 1.5$, $\beta_2 = 1.1$, $c = 5.0$; (Left) Phase plane and isolines, (Right) A typical time domain plot of an “attempted invasion”

### 4. THE COMPETITION-COMMENSALISM MODEL WITH ANTICIPATION

Rather than use the approach of [6] where the anticipated values of variables are used continuously to implement strategy, the strategy considered in this section will mirror that originally envisaged by Rosen [23] and used in [4] where the anticipated value of a variable will trigger a control action if it is needed and leave the system unaltered
otherwise.

From Section 3, it is known that an invasion will automatically succeed, either when intraspecific competition is structurally dominant or the size of the invading technology is initially large. So in considering a management strategy to maximise the chances of invasion, it is sufficient to consider the case where invasion is impossible without intervention. When \( \beta > 1 \), but there are no positive coexistence points (or internal fixed points: i.e. the parameter \( c \) does not satisfies (22)), then the only way for an invasion to succeed is for a permanent change in the coupling parameter which replaces \( \beta_2 \) by \( \hat{\beta}_2 < 1 \). This may put unrealistic demands on the resources available to the invader. However in the case where \( \beta_0 > 1 \) and there are positive coexistence points (i.e. \( c \) satisfies (22) so that there exists a saddle \( \mathbf{x}_{4,5} \) and a stable fixed point \( \mathbf{x}_{4,N} \) it may still be possible to successfully invade with limited resources even when the initial size of the invading technology is small.

A mathematical description of one such control strategy is “as long as the size of the invading technology is such that the trajectory lies in \( \mathcal{B}(\mathbf{x}_2) \), apply a correction to the coupling parameter that replaces \( \beta_2 \) by \( \hat{\beta}_2 < 1 \), otherwise leave \( \beta_2 \) as it is.” The stable manifold \( W^S \) of \( \mathbf{x}_{4,5} \) acts as the separatrix between the basins of \( \mathbf{x}_2 \) and \( \mathbf{x}_{4,N} \). It can be shown that the positive stable fixed point associated with the parameter \( \hat{\beta}_2 \) always lies “above” \( W^S \). Thus the strategy is guaranteed to get the trajectory into the basin of \( \mathbf{x}_{4,N} \) before \( \hat{\beta}_2 \) is turned on again and both technologies will then converge to \( \mathbf{x}_{4,N} \).

Representing \( W^S \) by \( \{ (x,y); W(x,y) = 0 \} \), and \( \mathcal{B}(\mathbf{x}_2) = \{ (x,y); W(x,y) < 0 \} \) and \( \mathcal{B}(\mathbf{x}_{4,N}) = \{ (x,y); W(x,y) > 0 \} \) respectively, the strategy can be described by

\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k) \\
y_{k+1} &= y_k + r_2 y_k \left( 1 - \frac{y_k}{1 + cx_k} \right) - \left\{ \begin{array}{ll} 
\hat{\beta}_2 x_k, & \text{if } W(x_k, y_k) < 0; \\
\beta_2 x_k, & \text{otherwise}
\end{array} \right.
\end{align*}
\]

A simulation of this strategy is shown in Fig. (6)

**FIGURE 6.** Modified LVC model with switching control - Invasion: \( r_1 = 1.8, \beta_1 = 0.2, r_2 = 1.5, \beta_2 = 1.1, \hat{\beta}_2 = 0.9, c = 9.0 \); (Left) Phase plane, isoclines and separatrix, (Right) A typical time domain plot of an successful invasion

It might be argued that computing \( W^S \) might not be feasible given the limited accuracy of the parameter values that are likely to be available in practice. However noticing that, in the basin of \( \mathbf{x}_2 \), being attracted to that stable fixed point necessarily means that \( y_k \) is decreasing, while in the basin of \( \mathbf{x}_{4,N} \), being attracted to \( \mathbf{x}_{4,N} \) means that \( y_k \) is increasing when it moves above \( W^S \). This leads to a more manageable control strategy : “As long as \( y_k \) is decreasing, apply a correction to the coupling parameter that replaces \( \beta_2 \) by \( \hat{\beta}_2 < 1 \), otherwise leave \( \beta_2 \) as it is.” This control can be implemented in an anticipative fashion : “As long as the predicted next value of \( y_k \) is less than the current value of \( y_k \),
apply a correction to the coupling parameter that replaces $\beta_2$ by $\hat{\beta}_2 < 1$, otherwise leave $\beta_2$ as is.” Symbolically, the system with anticipative control can be represented as: The “internal model” equations (whose variables are again distinguished by a tilde), and which coincide with the original modified LVC model, are

\[
\begin{align*}
\tilde{x}_{k+1} &= \tilde{x}_k + \tilde{r}_1 \tilde{x}_k (1 - \tilde{x}_k - \beta_1 \tilde{y}_k) \\
\tilde{y}_{k+1} &= \tilde{y}_k + \tilde{r}_2 \tilde{y}_k \left( 1 - \frac{\tilde{y}_k}{\tilde{y}_k + c \tilde{x}_k} - \beta_2 \tilde{x}_k \right)
\end{align*}
\] (12)

The 1-step output of the internal model is fed into the system equations to give:

\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k \left( 1 - x_k - \beta_1 y_k \right) \\
y_{k+1} &= y_k + r_2 y_k \left( 1 - y_k - \left\{ \begin{array}{ll} 
\hat{\beta}_2 x_k, & \text{if } \tilde{y}_{k+1} < y_k; \\
\beta_2 x_k, & \text{otherwise}
\end{array} \right. \right)
\end{align*}
\] (14)

A simulation of this strategy is shown in Fig(7).

FIGURE 7. Modified LVC model with anticipative switching control - Invasion: $r_1 = 1.8$, $\beta_1 = 0.2$, $r_2 = 1.5$, $\beta_2 = 1.1$, $\hat{\beta}_2 = 0.95$ (spurious fixed point), $\hat{\beta}_2 = 0.96$, $c = 9.0$; Typical time domain plots of successful invasions.

The strategy of making a decision based on comparing where the invader lies with respect to the separatrix always seems to work and the additional resources needed to invade are expended over a limited time period.

However the anticipatory strategy of deciding based on whether the invading technology is decreasing or increasing by comparing its current size with its predicted next size can sometimes lead to success with both technologies converging to the stable positive fixed point at $x_{4,N}$, and at other times lead to apparent success with coexistence between technologies but at a “spurious” fixed point.\(^3\) Which of these outcomes is seen is linked to the value of $\hat{\beta}_2$ used: the larger the value used, the more likely it is that the desired outcome (convergence to $x_{4,N}$) is seen, but at the cost of slower convergence. The strategy is successful in terms of only being used over a limited time span in this case; however in the other case with spurious outcomes, $\hat{\beta}_2$ is used throughout and there is never a reversion to the original value of $\beta_2$, thus invalidating the reasons for using such a strategy in the first place.

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\(^3\) Spurious fixed points are fixed points that do not exist in the original model, [3]
5. CONCLUSIONS

The competition-commensalism model analysed in the paper differs from the standard LVC model in that for sufficiently large values of the commensalistic parameter $c$, it exhibits a positive co-existence between the species (technologies) even when the interspecific competition or coupling parameters would indicate otherwise. However the co-existence state may be difficult to reach by invasion. In this scenario it may be hard for a new technology to put in place the conditions that would allow it to invade successfully. A simple anticipatory scheme is shown to offer a way-in for the invader, maybe at an acceptable price. It remains to estimate the parameter $c$ for some real data, and thus to see whether (22) can realistically be satisfied.

No attempt was made to see if having successfully invaded, the new technology would then subsequently replace the existing technology. In terms of the standard LVC model and also the modified LVC model, this would require that $\beta_1$ parameter change to be greater than 1, which would necessitate a different modelling approach.

It is also of interest to extend the modelling of the inter-technology rivalry by investigating what happens if the established technology also benefits from the advent of the newcomer.

Finally, even though LVC models have been fitted to real world data, [12],[27], not everyone agrees that they are as powerful a tool for predicting invasion or substitution as their protagonists would claim: “The classic Lotka-Volterra equations [2], [18], [19] and [20] present a method for estimating market share capture by a new product or technology given an existing product or technology. Unfortunately the equation parameters, including a number of variables representing symbiotic interactions between two technologies or products, have not been well-enough-defined to allow one to estimate their values given empirical or hypothetical observations”.[7]. This objection has to be answered for the modified LVC model also.

A1 FIXED POINTS OF PLANAR MAPS

The trajectory of the map\(^4\)

\[
\begin{align*}
x_{k+1} &= f(x_k, y_k), \\
y_{k+1} &= g(x_k, y_k).
\end{align*}
\]

\(16\)

is \(\{(x_k, y_k), k \geq 0\}\). \(\mathbf{x} = (x, y)\) is a fixed point of (16) if it satisfies the equations \(x_{k+1} = x_k\) and \(y_{k+1} = y_k\). The curves defined by \(x_{k+1} = x_k\) or \(y_{k+1} = y_k\) are called zero growth isoclines, herein shortened to isoclines.

A fixed point is locally (asymptotically) stable if trajectories starting near it converge to it with increasing time. A sufficient condition for this to occur is if all its multipliers (the eigenvalues of the Jacobian matrix of the map evaluated at the fixed point) have magnitude less than 1. The set of trajectories that are attracted to a stable fixed point is called the basin of the fixed point and is denoted \(B(x)\). The Jacobian matrix of (16) is

\[
J = \begin{pmatrix}
\frac{\partial f}{\partial x}(x, y) & \frac{\partial f}{\partial y}(x, y) \\
\frac{\partial g}{\partial x}(x, y) & \frac{\partial g}{\partial y}(x, y)
\end{pmatrix}
\]

\(17\)

If either of the multipliers has magnitude greater than 1, then the fixed point is unstable. If one of the multipliers has magnitude less than 1 and the other magnitude greater than 1, then the fixed point is called a saddle point. Each saddle has a stable manifold \(W^S\) which is the set of trajectories which converge to the saddle with increasing time: generically \(W^S\) is a curve.

A2 FIXED POINTS OF COMPETITION MAPS

The LVC map (2) and modified LVC map (9) are described by

\[
\begin{align*}
x_{k+1} &= x_k + r_1 x_k (1 - x_k - \beta_1 y_k), \\
y_{k+1} &= y_k + r_2 y_k (1 - \frac{y_k}{1 + cx_k} - \beta_2 x_k).
\end{align*}
\]

\(18\)

\(^4\) General ideas about discrete dynamical systems can be found in, for instance, [28].
where all the parameters are positive (with \( c = 0 \) for the LVC map). The *Jacobian* matrix is

\[
J = \begin{pmatrix}
1 + r_1(1 - 2x - \beta_1y) & -r_1\beta_1x \\
2c\frac{\gamma x^2}{(1+cx)^2} - r_2\beta_2y & 1 + r_2(1 - 2\frac{\gamma y}{1+cx} - \beta_2x)
\end{pmatrix}
\]

The fixed points of this model with their associated *Jacobian* matrices are readily computed to be

\[
x_1 = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad J_1 = \begin{pmatrix} 1 + r_1 & 0 \\ 0 & 1 + r_2 \end{pmatrix}
\]

\[
x_2 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad J_2 = \begin{pmatrix} 1 - r_1 & -r_1\beta_1 \\ 0 & 1 + r_2(1 - \beta_2) \end{pmatrix} \tag{19}
\]

\[
x_3 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad J_3 = \begin{pmatrix} 1 + r_1(1 - \beta_1) & 0 \\ r_2(\beta - \beta_2) & 1 - r_2 \end{pmatrix}
\]

and the off-axes fixed point \( x_4 = (x^*, y^*) \) where \( x^* \) and \( y^* \) satisfy

\[
1 - x^* - \beta_1y^* = 0, \quad 1 - \frac{y^*}{1+cx^*} - \beta_2x^* = 0 \tag{20}
\]

has *Jacobian* matrix

\[
J_4 = \begin{pmatrix} 1 - r_1x^* & -r_1\beta_1x^* \\
r_2c\frac{(y^*)^2}{(1+cx^*)^2} - r_2\beta_2y^* & 1 + r_2\frac{y^*}{1+cx^*} \end{pmatrix}
\]

Depending on parameter values, \( x_4 \) may or may not be biologically feasible, i.e. both species having positive values, which will be called a positive solution. When \( c = 0 \) (and \( \beta_1\beta_2 \neq 1 \)), \( x_4 \) is

\[
\begin{pmatrix} x^* \\ y^* \end{pmatrix} = \begin{pmatrix} \frac{1 - \beta_1}{1 - \beta_1\beta_2} \\ \frac{1 - \beta_2}{1 - \beta_1\beta_2} \end{pmatrix} \tag{21}
\]

When \( c \neq 0 \), (20) has one positive solution when \( \beta_1 < 1, \beta_2 < 1 \), and two positive solutions when \( \beta_1 < 1, \beta_2 \geq 1 \) and

\[
c \geq \left( \sqrt{\beta_2(1/\beta_1 - 1)} + \sqrt{1/\beta_1(\beta_2 - 1)} \right)^2. \tag{22}
\]

In addition, it has one positive solution when \( \beta_1 \geq 1, \beta_2 > 1 \) and no positive solutions otherwise.

### A3 INVASION CRITERION

The standard approach to determining invasion criteria is to consider the situation where one of the species is absent (say \( y_k \)), the other (\( x_k \)) is in or near equilibrium at its carrying capacity, and then to introduce a small number of species \( y_k \) and investigate under what conditions this number grows with time.

Consider the model of Appendix A2. At the fixed point \( x_2, x_k \) is stable at its carrying capacity \( x_k = 1 \) provided

\[
0 < r_1 < 2, \text{ and } y_k \text{ is absent} - \text{see (19)}. \text{ From (18) } y_{k+1} > y_k \text{ provided } 1 - y_k / (1 + cx_k) - \beta_2y_k > 0 \text{ and at } x_2 \text{ this is equivalent to } 1 - \beta_2 > 0. \text{ Thus } y_k \text{ can invade if } \beta_2 < 1. \text{ Inspection of (19) shows that means the second multiplier of } x_2 \text{ is greater than 1. Thus } y_k \text{ being capable of invading is equivalent to } x_2 \text{ being unstable, or more particularly, to } x_2 \text{ being a saddle.}^5 \text{ This is a well known property of LVC models, but is not generally true for other models, [16].}

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^5 In the case where \( c = 0 \) and \( \beta_1 > 1 \), \( x_2 \) is a saddle whenever \( r_2 > \frac{\sqrt{\beta_2}}{\beta_1} \). However this can be ignored as it leads to the biologically infeasible trajectories discussed previously.
REFERENCES