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Stability Analysis of a Three-Species, Multi-Patch Variant of the Lotka-Volterra Model

Carl Barratt

Correspondence: Prof. Emeritus of Mechanical Engineering, University of New Haven, West Haven, CT, USA

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Abstract

We investigate the stability of the steady-state behavior of a variant of the classic Lotka-Volterra predator-prey model. The variant, LV(3,n), involves three interacting species distributed among n patches with diffusive interaction between the patches; one of the species is allowed to migrate between adjacent patches. Criteria on the phase-space of the three interaction constants are determined to ensure stability of the population steady-states.

Keywords: Autocatalytic chemical reactions, Lotka-Volterra, Lyapunov stability, Routh-Hurwitz analysis, patches, diffusion/migration

1. Introduction

The classic 2-species, 1-patch Lotka-Volterra (LV) model was first proposed by Alfred J. Lotka (1910 & 1920) to study autocatalytic reactions and used later by Lotka (1925) to model the nonlinear biological interaction of a predator and its prey confined to a single patch of land. The same equations were published by Vito Volterra (1926) in his marine biology investigations. Thereafter, the equations and their extensions, provided a basis for countless studies in a variety of fields in chemistry, biology and ecology. Recent examples of such studies include an analysis of the global dynamics of a 2-species system with asymmetric dispersal/migration (Chen et. al. 2022); a 2-patch system in which both species migrate (Feng et. al. 2011); a 2-patch, 2-species system in which dispersal depends on predator strength (Kang et. al. 2017); a competition between resident and mutant species in a 2-river network (Liu et. al. 2024); and a stability analysis of a 2-patch, 2-species system with built in dispersal delays (Sun & Mai. 2018).

In the present paper we explore a variant of the aforementioned systems by considering a 3-species extension of the LV model; furthermore, the species occupy n patches forming a closed system and allow diffusion/migration of one of the three species between adjacent patches.

The layout of the paper is as follows: Section 1 includes a brief review of the LV model, including a Lyapunov stability analysis (Lyapunov A.M, 1892) that will be used in later sections. In section 2 we introduce the variant LV(3,1) of the classic LV, involving three species, x, y, a, enclosed in a single patch, with the time-dependent dynamics governed by three *reaction* constants k_1, k_2, k_3. Using Lyapunov analysis, we investigate the steady-state in which all three species acquire constant non-zero asymptotic values (x^*, y^*, a^*), to determine the criteria on k_1, k_2, k_3 necessary to ensure steady-state stability. In section 3, the discussion is extended to analyze LV(3,2); the three species are initially randomly distributed between two patches, coupled to allow migration of species “a” between the patches. Lyapunov analysis together with Routh-Hurwitz matrix analysis (RH) (Routh, E.J, 1877; Hurwitz, A, 1895; and Bodson.M, 2020 for recent description of the method) are used to investigate stability of the steady-state (x^*, y^*, a^*). In sections 4,5,6 the analysis is extended to that of LV(3,3), LV(3,4), and LV(3,5). In anticipation of LV(3,n>5), section 6 introduces a mathematical trick critical to circumventing the need to handle bewilderingly large RH matrices: We show that the governing eigenvalue (determinantal) eqn. can be factorized in such a way that the RH analysis can indeed be restricted to a manageable size matrix analysis. Section 6 exploits the factorization to derive a *general* closed-form criterion for the values of k_1, k_2, k_3 for stability of the steady-state and applies it to an analysis of LV(3,6). Finally, in section 7, we summarize how to apply the derived criteria to the general case of LV(3,n); this section includes analysis of the n=7 & 8 cases by way of illustrating the methodology.

1. A quick review of the classic Lotka-Volterra model with one predator, y (fox), one prey, x (hare).

The equations governing the evolution of population of predator and prey are the classic

$$\frac{dx}{dt} = (\alpha - \beta y)x, \qquad \frac{dy}{dt} = (\gamma x - \delta)y \tag{1.1}$$

What are these eqns, including the four positive constants α,β,γ,δ, telling us about the interaction between the hares and foxes? Essentially, hares (x) eat grass and flourish (α), foxes (y) eat hares and flourish (γ) at the expense of the hare population (β). As the hare population diminishes, the foxes are challenged by the loss of sustenance in addition to natural die off or emigration (δ). Consequently the hare population revives and with it an increased opportunity for the foxes… and the cycle repeats.

The stability of the non-trivial fixed point (FP) of the governing Eqs.(1.1) at (x*,y*) = (δ/γ, α/β) dictates the evolution of the hare and fox populations. The most direct way to investigate this stability is using Lyapunov analysis: We perturb the equations about the FP,

$$\frac{d(\delta x)}{dt} = -\frac{\beta\delta}{\gamma}(\delta y) = \lambda(\delta x) \tag{1.2.1}$$

$$\frac{d(\delta y)}{dt} = \frac{\gamma\alpha}{\beta}(\delta x) = \lambda(\delta y) \tag{1.2.2}$$

in which λ designates a Lyapunov exponent. In general, λ will be a complex number; if its real part is positive, it is clear from Eqs.(1.2) that the perturbation exponentially deviates/explodes away from the fixed point, which is consequentially unstable. Conversely, a negative real part suggests the opposite. For the above basic LV system we see that the perturbed Eqs. (1.2) yield $\lambda^2 + \alpha\delta = 0,\ \lambda = \pm i\sqrt{\alpha\delta}$. Since these solutions are both pure imaginary (no real parts) and conjugate to each other, the FP is *elliptic* and the governing equations yield solutions that are stable but not constant, Fig.1; rather a small perturbation produces an elliptical orbit that remains close to the FP, I.e. the x, y populations are periodic and undamped, oscillating on an ellipse in (x,y) space with frequency $\omega = \sqrt{\lambda_1\lambda_2} = \sqrt{\alpha\delta}$, period T= 2π/ω. While the time dependence of x and y can only be extracted numerically, it can be eliminated between the equations, viz:

$$\frac{dx}{dy} = \frac{(\alpha-\beta y)x}{(\gamma x-\delta)y} \tag{1.3}$$

which, upon rearrangement and integration, generates the following constraint between x and y:

$$x^{\delta}y^{\alpha}e^{-\gamma x}e^{-\beta y} = K \tag{1.4}$$

in which larger K values correspond to orbits closer to the FP, (δ/γ, α/β), at which point

$$K = K_{max} = (\frac{\delta}{e\gamma})^{\delta}(\frac{\alpha}{e\beta})^{\alpha}.$$

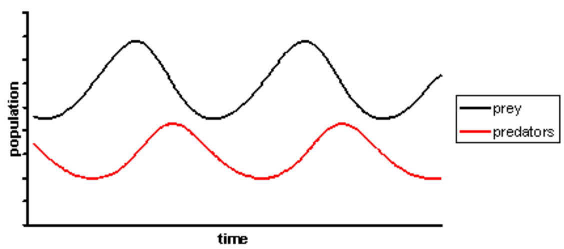

Figure 1. Evolution of predator prey populations in the classic Lotka-Volterra system

2. A variation on the LV theme; 3 species in 1 patch, LV(3,1)

Consider the following variation on the classic LV system, involving three variables x(t), y(t), a(t) henceforth denoted LV(3,1) and describing the interaction of 3 species confined to 1 patch:

$$\frac{dx}{dt} = (k_1 a - k_2 y)x, \quad \frac{dy}{dt} = (k_2 x - k_3)y, \quad \frac{da}{dt} = k_3 y - k_1 ax \tag{2.1}$$

In the context of chemical kinetics the above LV equations describe the *autocatalytic* system

$$a + x \to 2x, \quad x + y \to 2y, \quad y \to a \tag{2.2}$$

with respective reaction constants k_1, k_2, k_3. In the present context of predator-prey, we can think of x as prey to predator y and a as prey to predator x but also a is a predator to y. But clearly, the system of Eqs. (2.1) is different from classic LV in that it is "closed", namely dx/dt + dy/dt + da/dt =0 meaning that the total population x+y+a = ∑ is constant. Another difference is that the non-trivial fixed point FP (a*, x*, y*) = (a*, k_3/k_2, a*k_1/k_2) is, under specified conditions, stable, i.e. represent asymptotically *constant* populations of a, x, y. To investigate these conditions we again invoke Lyapunov: Perturbing Eqs.(2.1) about the FP yields

$$\frac{d\delta x}{dt} = -k_3\delta y + \frac{k_1k_3}{k_2}\,\delta a = \lambda\delta x \tag{2.3.1}$$

$$\frac{d\delta y}{dt} = k_1 a^*\delta x = \lambda\delta y \tag{2.3.2}$$

$$\frac{d\delta a}{dt} = -k_1a^*\delta x + k_3\delta y - \frac{k_1k_3}{k_2}\,\delta a = \lambda\delta a \tag{2.3.3}$$

and the Lyapunov exponents λ_1, λ_2, λ_3 are solutions of the (determinantal) eigenvalue equation

$$\mathrm{Det}\begin{vmatrix} -\lambda & -k_3 & (k_1k_3/k_2) \\ k_1a^* & -\lambda & 0 \\ -k_1a^* & k_3 & -[\lambda + (k_1k_3/k_2)] \end{vmatrix} = 0 \tag{2.4}$$

Thus, the three λ's are solutions of

$$\lambda[\lambda^2 + \lambda\,(k_1k_3/k_2) + k_1k_3a^*(1 + k_1/k_2)] = 0 \tag{2.5}$$

For the sake of convenience for discussion of further extensions of this system to multiple patches, we can make the transformation $\lambda \to \lambda\ (k_1k_3/k_2)$ and define ξ, η, b via

$$\xi = \lambda^3 + \lambda^2 + \lambda\eta\left(1 + \frac{k_1}{k_2}\right) + \eta, \qquad \text{with} \qquad \eta = \frac{a^*{k_2}^2}{k_1k_3} \ and\ \eta\left(1 + \frac{k_1}{k_2}\right) = b$$

in terms of which Eq.(2.5) can be written

$$\xi - \eta = 0 \tag{2.6}$$

Since all coefficients in Eq.(2.5) are positive, both λ's have negative real parts, sufficient to ensure stability of the FP and corresponding *constant* asymptotic populations (flatlines) of a, x, y, for all values of the k's. Actually, this needs to be qualified since we have to also consider the conservation constraint ∑ = constant, with

$$\textstyle\sum = a(0)+x(0)+y(0) = a(t)+x(t)+y(t) = a^* + x^* + y^* = k_3/k_2+a^*(1+k_1/k_2) \tag{2.7}$$

which imposes the constraint $k_3/k_2 < \sum$ since a* is necessarily > 0. The reader is encouraged to show that $k_3/k_2 > \sum$ leads to a trivial fixed point (x*, 0, 0) and to verify the behavior of the system in this part of parameter space by numerically solving the governing Eqs.(2.1).

We also notice, in passing, the interesting special case, $k_1 = 0$,

$$\frac{dx}{dt} = -k_2yx, \quad \frac{dy}{dt} = (k_2x - k_3)y, \quad \frac{da}{dt} = k_3y \tag{2.8}$$

equations of particular interest to epidemiologists since they are the very same SIR equations that form the basis of studies of pandemics (e.g. COVID 19)! In the form of Eqs.(2.8) x, y, a respectively represent the fractions of the population that are Susceptible (S), Infected (I), and Recovered (or deceased) (R). The interested reader is referred to H. Hethcote's [2000] comprehensive review of such infectious-disease models. It might be interesting to use the methods of the current paper to an investigation of SIR (and its variants) for multiple *communities* - coupled by *migration* – but this special case ($k_1 = 0$), is not pursued here.

3. Three species occupying n=2 patches with dispersion between the patches. LV(3,2)

The autocatalytic system of Eqs.(2.2) is now generalized to

$$a_1 + x_1 \to 2x_1 \quad (k_1)$$
$$x_1 + y_1 \to 2y_1 \quad (k_2)$$
$$y_1 \to a_2 \quad (k_3)$$
$$\tag{3.1}$$
$$a_2 + x_2 \to 2x_2 \quad (k_1)$$

$$x_2 + y_2 \rightarrow 2y_2 \quad (k_2)$$
$$y_2 \rightarrow a_1 \quad (k_3)$$

corresponding to governing equations

$$\frac{dx_1}{dt} = (k_1a_1 - k_2y_1)x_1, \quad \frac{dy_1}{dt} = (k_2x_1 - k_3)y_1, \quad \frac{da_1}{dt} = k_3y_2 - k_1a_1x_1 \tag{3.2.1}$$

$$\frac{dx_2}{dt} = (k_1a_2 - k_2y_2)x_2, \quad \frac{dy_2}{dt} = (k_2x_2 - k_3)y_2, \quad \frac{da_2}{dt} = k_3y_1 - k_1a_2x_2 \tag{3.2.2}$$

Notice, the three populations a,x,y are now divided between two patches according to the randomly chosen initial (t=0) values of each, $x_1(0)\ldots.a_2(0)$; also members of the "a" population are allowed to disperse/migrate between the two patches. Again we note that the total population $\sum = x_1 + y_1 + \ldots.. + a_2$ is constant since the system is closed, with $dx_1/dt + \ldots. + da_2/dt = 0$.

To investigate the stability of the fixed point (FP) $x_1^* = x_2^* = x^* = k_3/k_2$, $y_1^* = y_2^* = y^* = a^*k_1/k_2$, $a_1^* = a_2^* = a^*$, we employ the Lyapunov routine as before, perturbing the system Eqs.(3.2) to generate a 6 x 6 determinantal eigenvalue equation

$$\begin{bmatrix} -\lambda & 0 & -k_3 & 0 & 0 & k_1k_3/k_2 \\ 0 & -\lambda & 0 & -k_3 & k_1k_3/k_2 & 0 \\ k_1a^* & 0 & -\lambda & 0 & 0 & 0 \\ 0 & k_1a^* & 0 & -\lambda & 0 & 0 \\ 0 & -k_1a^* & k_3 & 0 & -(\lambda + k_1k_3/k_2) & 0 \\ -k_1a^* & 0 & 0 & k_3 & 0 & -(\lambda + k_1k_3/k_2) \end{bmatrix} = 0 \tag{3.3}$$

which in turn, after some manipulation, can be reduced, using the ξ, η defined above, to the 2 x 2 form

$$\begin{vmatrix} \xi & -\eta \\ -\eta & \xi \end{vmatrix} = \xi^2 - \eta^2 = 0 \tag{3.4}$$

or equivalently,

$$\left(\lambda^3 + \lambda^2 + \lambda\eta\left(1 + \frac{k_1}{k_2}\right) + \eta\right)^2 - \eta^2 = 0 \tag{3.5}$$

Before pursuing use of Eq.(3.5) to investigate stability of the FP for the above 2-patch system, we note a "pattern", namely n=1 led to $\xi - \eta = 0$, and n=2 leads to $\xi^2 - \eta^2 = 0$. Can it be that for n patches this generalizes to

$$\xi^n - \eta^n = 0? \tag{3.6}$$

It turns out that the answer to this question is *yes*; the proof, an exercise in manipulation of determinants is left to the reader.

Returning to our analysis of the n=2 system we expand Eq.(3.5) into the form

$$\lambda^6 + 2\lambda^5 + \lambda^4(1 + 2b) + 2\lambda^3(\eta + b) + \lambda^2(b^2 + 2\eta) + 2\lambda b\eta = 0 \tag{3.7}$$

where, as previously defined,

$$b = \eta\left(1 + \frac{k_1}{k_2}\right), \quad \eta = \frac{a^*{k_2}^2}{k_1k_3} \tag{3.8}$$

We recall that stability of the FP requires that every one of the 6 λ solutions of Eq.(3.7) must have a –ve (or zero) real part. Obviously, obtaining solutions of the polynomial Eq.(3.7) throughout the phase space of the k's is foreboding. Fortunately, we don't need to determine the explicit solutions since we have available another powerful tool, used widely in the study of feedback control systems, namely the Routh-Hurwitz (RH) routine, illustrated as follows: Writing Eq. (3.7) in the form $\lambda^6 + f_1\lambda^5 + f_2\lambda^4 + f_3\lambda^3 + f_4\lambda^2 + f_5\lambda^1$, the RH routine requires us to form the following matrix:

$$\begin{array}{lll} 1 & f_2 & f_4 \\ f_1 & f_3 & f_5 \\ a_{31} = f_1f_2 - 1f_3 & a_{32} = f_1f_4 - 1f_5 & 0 \\ a_{41} = a_{31}f_3 - f_1a_{32} & a_{42} = a_{31}f_5 & 0 \\ a_{51} = a_{41}a_{32} - a_{31}a_{42} & 0 & 0 \end{array} \tag{3.9}$$

The first entry of each row is of particular interest since the RH routine simply requires that there be NO change of sign from one row to the next for the fixed point (FP) under investigation to be stable.

Using Eq.(3.7) the entries a_{i1} follow simply: $a_{11} = 1$, $a_{21} = 2$, $a_{31} = 2(1+b-\eta) = 2(1 + \eta k_1/k_2)$; all positive with no change of sign thus far. Proceeding, a_{41} simplifies to the factorized form

$a_{41} \sim (b-\eta)(1+\eta) = (k_1/k_2)\,\eta(1+\eta)$, again >0. Finally, the entry a_{51} can be written

$a_{51} \sim (b-2\eta)[(b-\eta)^2 + \eta] = (k_1/k_2 - 1)\eta[(b-\eta)^2 + \eta]$. Thus, RH has yielded the simple requirement $k_1/k_2 > 1$ for stability of the n=2 FP. In addition to this constraint we also have to satisfy the conservation constraint, which for the n=2 case now reads $\sum = 2\,[k_3/k_2 + a^*(1+k_1/k_2)]$ so imposes the additional constraint $k_3/k_2 < \sum/2$.

In summary, for the n=2 case we have flatline steady-state populations $x^* = k_3/k_2$, $y^* = a^* k_1/k_2$, and $a^* = [\sum/2 - k_3/k_2]/(1+k_1/k_2)$ and stability requires $k_1/k_2 > 1$ (from RH) and $k_3/k_2 < \sum/2$ (from conservation).

Before proceeding to n>2, we note that, while the above RH algebra was straightforward, it could have been simplified substantially by noting that $\xi^2 - \eta^2 = (\xi - \eta)(\xi + \eta)$, in which $(\xi - \eta)$ is simply the n=1 case whose stability has already been guaranteed, and RH can now be applied to $(\xi + \eta) = \left(\lambda^3 + \lambda^2 + \lambda\eta\left(1 + \frac{k_1}{k_2}\right) + 2\eta\right)$ to yield immediately the matrix

$$\begin{array}{ll} 1 & \eta\left(1 + \frac{k_1}{k_2}\right) \\ 1 & 2\eta \\ a_{31} = \eta(k_1/k_2 - 1) & \end{array} \tag{3.10}$$

and the required constraint $k_1/k_2 > 1$ obtained above.

4. The n=3 Patches Case, LV(3,3)

The system now reads

$$\begin{array}{c} a_1 + x_1 \to 2x_1 \quad (k_1) \\ x_1 + y_1 \to 2y_1 \quad (k_2) \\ y_1 \to a_2 \quad (k_3) \\ \\ a_2 + x_2 \to 2x_2 \quad (k_1) \\ x_2 + y_2 \to 2y_2 \quad (k_2) \\ y_2 \to a_3 \quad (k_3) \\ \\ a_3 + x_3 \to 2x_3 \quad (k_1) \\ x_3 + y_3 \to 2y_3 \quad (k_2) \\ y_3 \to a_1 \quad (k_3) \end{array} \tag{4.1}$$

and the corresponding system equations describing the evolution of the populations x,y,a read

$$\frac{dx_1}{dt} = (k_1 a_1 - k_2 y_1)x_1,\quad \frac{dy_1}{dt} = (k_2 x_1 - k_3)y_1,\quad \frac{da_1}{dt} = k_3 y_3 - k_1 a_1 x_1$$

$$\frac{dx_2}{dt} = (k_1 a_2 - k_2 y_2)x_2,\quad \frac{dy_2}{dt} = (k_2 x_2 - k_3)y_2,\quad \frac{da_2}{dt} = k_3 y_1 - k_1 a_2 x_2 \tag{4.2}$$

$$\frac{dx_3}{dt} = (k_1 a_3 - k_2 y_3)x_2,\quad \frac{dy_3}{dt} = (k_2 x_3 - k_3)y_3,\quad \frac{da_3}{dt} = k_3 y_2 - k_1 a_3 x_3$$

Factoring $\xi^3 - \eta^3$ into the form $\xi^3 - \eta^3 = (\xi - \eta)(\xi^2 + \xi\eta + \eta^2)$ we need only apply R-H analysis to the piece

$$(\xi^2 + \xi\eta + \eta^2) = \lambda^6 + 2\lambda^5 + (1+2b)\lambda^4 + \ldots + 3\eta^2 \tag{4.3}$$

To yield an array

1	$1+2b$	$b^2+3\eta$	$3\eta^2$
2	$2b+3\eta$	$3b\eta$	
a_{31}	…	…	
a_{41}	…		
a_{51}	…		
a_{61}			

(4.4)

The entries $a_{31} = 2b+2-3\eta = 2+(2k_1/k_2 -1)\eta$ and $a_{41} = (2 k_1/k_2 - 1)\eta(2+3\eta)$ establish the stability requirement $k_1/k_2 > ½$. The entry a_{51} becomes $a_{51} = 2\eta(2 k_1/k_2 - 1) [2(k_1/k_2)^2 - 5 k_1/k_2 + 8] + 12 k_1/k_2$ so that, since [ ] > 0, the bound on k_1/k_2 already guarantees $a_{51} > 0$. Finally, the entry a_{61} may be written in the factorized form

$$a_{61} = \eta^2 [(2 k_1/k_2 - 1)^2 - 2/\eta][(2 k_1/k_2 -1) + 2/\eta][(k_1/k_2)^2 - k_1/k_2 +1] \quad (4.5)$$

Given the constraint on k_1/k_2, the second and third [ ] brackets are clearly positive, leaving the first bracket which imposes the additional constraint, this time on $\eta = \frac{a^* {k_2}^2}{k_1 k_3}$, namely

$$1/\eta < 2(k_1/k_2 - ½)^2 = \Omega \quad (4.6)$$

Finally, we have the conservation requirement

$$\sum = 3 [k_3/k_2+a^*(1+k_1/k_2)] \quad (4.7)$$

from which we deduce the constraint

$$k_3/k_2 < (\sum/3)/[1+ (k_1/k_2)(1+ k_1/k_2)/ \Omega] \quad (4.8)$$

and the asymptotic population of species a, namely $a^* = [\sum/3 - k_3/k_2]/ (1+k_1/k_2)$.

The n=3 stability requirements determined above, along with the asymptotic values of x, y, a, are easily verified by numerically solving the governing equations.

5. n=4 patches, LV(3,4)

Given the factorized form of $\xi^4 - \eta^4 = (\xi^2 - \eta^2)(\xi^2 + \eta^2)$ we obtain from $\xi^2 - \eta^2$ the n=2 constraint $k_1/k_2 >1$, and the RH analysis of $\xi^2 + \eta^2$ generates the additional constraint

$$1/\eta < (k_1/k_2)^2 = \Omega' \quad (5.1)$$

The n=4 version of Eq.(4.8) yields $k_3/k_2 < (\sum/4)/[1+ (k_1/k_2)(1+ k_1/k_2)/ \Omega']$ and for chosen k_3/k_2, a* follows from

$a^* = [\sum/4 - k_3/k_2]/ (1+k_1/k_2)$.

6. *n=5 and beyond, LV(3,≥5)*

Thus far, the cases n=1,2,3,4 have been algebraically manageable, giving us confidence to move onto n=5. We start with the factored form $\xi^5 - \eta^5 = (\xi-\eta)(\xi^4 + \xi^3\eta + \xi^2\eta^2 + \xi\eta^3 + \eta^4)$ but this still requires coping with an order λ^{12} polynomial! The RH array has 12 rows. Clearly the algebra involved in generating the 1st column entries $a_{31}, a_{41},\ldots, a_{12,1}$ is foreboding, especially given the need to simplify – via factorization or otherwise – the entries so as to expose stability constraints on k_1/k_2 , k_3/k_2, and η. Furthermore, having achieved results for n=5 we would like to go further and generalize to n=n.

Fortunately, the mathematics provides a trick by revealing to us that $\xi^n - \eta^n$ can be written in one of two factorized forms, depending on n, viz:

For n=odd,

$$\xi^n - \eta^n = (\xi-\eta)(\xi^2 - \omega_1\xi\eta + \eta^2)(\xi^2 - \omega_2\xi\eta + \eta^2)\ldots (\xi^2 - \omega_{(n-1)/2} \xi\eta + \eta^2) \quad (6.1)$$

For n=even,

$$\xi^n - \eta^n = (\xi^2-\eta^2)(\xi^2 - \omega_1\xi\eta + \eta^2)(\xi^2 - \omega_2\xi\eta + \eta^2)\ldots (\xi^2 - \omega_{(n-2)/2} \xi\eta + \eta^2) \quad (6.2)$$

in which the coefficients ω_1, ω_2 etc. can be easily determined and will turn out to be bounded by $-2<\omega<2$; we'll see how in section 7, below. The point is that, having determined the ω's, the stability analysis of the general case of n patches reduces to application of RH to the polynomial $(\xi^2 - \omega\xi\eta + \eta^2)$, so is no more onerous than that of the n=3 analysis above! Proceeding with RH analysis of the factor $(\xi^2 - \omega\xi\eta + \eta^2)$, with $\xi = \lambda^3 + \lambda^2 + \lambda\eta b + \eta$, we quickly obtain the first 2 rows of RH entries

1	$1+2b$	$(2-\omega)\eta + b^2$	$(2-\omega)\eta^2$
2	$(2-\omega)\eta+2b$	$(2-\omega)b\eta$	

(6.3)

a_{31} quickly follows, $a_{31} = 2+2(k_1/k_2 + \omega/2)\eta$, and we obtain $a_{41} = 4\eta(k_1/k_2 + \omega/2)(1+\eta(1-\omega/2))$, establishing the bound $(k_1/k_2 + \omega/2)>0$. For a_{51}, we obtain

$$\frac{1}{8}a_{51} = (\frac{k_1}{k_2}+\frac{\omega}{2})^3\eta^3 + 2\eta^3\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)\left(1-\frac{\omega}{2}\right) - [\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)^2\eta - \left(1+\frac{k_1}{k_2}+\omega\right)]\eta^2(1-\frac{\omega}{2})$$

but to convince ourselves that this is positive definite, it must be further manipulated to yield

$$a_{51} \sim (\frac{k_1}{k_2}+\frac{\omega}{2})\eta^3\left[\left(\frac{k_1}{k_2}+\frac{\omega}{2}-\frac{1}{2}\left(1-\frac{\omega}{2}\right)\right)^2 + \left(1-\frac{\omega}{2}\right)\left(2-\frac{1}{4}\left(1-\frac{\omega}{2}\right)\right)\right] + \eta^2\left(1-\frac{\omega}{2}\right)[\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)+1+\omega/2]$$

(6.4)

Given that $k_1/k_2 + \omega/2 > 0$ from a_{31} and $a_{41,}$ and also given (we'll see below) that all ω's in Eq.(6.4) are bounded above and below via $-2<\omega<2$, it follows that a_{51} is indeed positive definite. Thus, it just remains to determine $a_{61} = a_{51}a_{42}-a_{41}a_{52}$. We obtain eventually

$$a_{61} = 8\eta^3\left(1-\frac{\omega}{2}\right)\left(1+\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)\eta\right)\left[\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)^2+\left(1-\frac{\omega^2}{4}\right)\right]4\eta\left\{\left(\frac{k_1}{k_2}+\frac{\omega}{2}\right)^2\eta-(1+\frac{\omega}{2})\right\}$$

(6.5)

which is positive definite iff the last bracket { } is positive. Thus we have determined the all-important stability constraint relation

$$1/\eta < \Omega(\omega) = (k_1/k_2 + \omega/2)^2/(1+\omega/2) \quad (6.6)$$

which together with the constraints $k_1/k_2 + \omega/2 > 0$ and $\sum = n[k_3/k_2+a^*(1+k_1/k_2)] > 0$ would *seem* to represent the solution of our problem for the general n=n case.

However, we are not yet done. Eq.(6.1) involves (n-1)/2 ω's, i.e. we have to consider (n-1)/2 Ω's, each of which depends not only on ω but also on the chosen value of k_1/k_2. It follows from a_{61} that stability of the LV(3,n) FP requires $1/\eta < \Omega_{min}$, i.e. the *smallest* of the Ω's. Likewise,

Eq.(6.2) involves (n-2)/2 Ω's in addition to the $k_1/k_2 > 1$ constraint resulting from the $(\xi^2-\eta^2)$ factor.

The challenge now is to determine which is the smallest Ω, i.e. Ω_{min}.

To do this, consider again $(\xi^2 - \omega\xi\eta + \eta^2)=0$ and introduce angle θ via $\omega = 2\cos\theta$. This corresponds to $\xi = \eta e^{i\theta}$, and the corresponding $(\xi^n-\eta^n)/(\xi-\eta) \sim \sin(n\theta/2)/\sin(\theta/2)$ for n odd, and $(\xi^n-\eta^n)/(\xi^2-\eta^2) \sim \sin(n\theta/2)/\sin(\theta)$ for n even. The θ's follow from solving the appropriate expression $\sin(n\theta/2)/\sin(\theta/2) = 0$ or $\sin(n\theta/2)/\sin(\theta) = 0$ to obtain for n odd $\theta = 2/n$ (π, 2π, 3π,…(n-1)π/2) and for n even θ = (2/n)(π, 2π, 3π,…(n-2)π/2), resp. Recall again that for n even, the $(\xi^2-\eta^2)$ factor contributes the additional $(k_1/k_2 -1)>0$ constraint obtained for the n=2 case.

Defining $\beta_i = \omega_i/2 = \cos\theta_i$ we order the β's according to $\beta_1>\beta_2>\ldots$, e.g. for the case n=5 we would have $\beta_1 = \cos(2\pi/5) = 0.309$, $\beta_2 = \cos(4\pi/5) = -0.809$.

In terms of β, Ω is given by $\Omega = (k_1/k_2 + \beta)^2/(1+\beta)$. Now, for $\beta_i > \beta_j$ we determine the condition on k_1/k_2 that yields $\Omega_i < \Omega_j$, i.e. $\Omega_j - \Omega_i > 0$. We obtain the condition $k_1/k_2 > 1 + \sqrt{[(1+\beta_i)(1+\beta_j)]}$. More generally, we obtain

For $\beta_i > \beta_j$, $\Omega_i < \Omega_j$ requires $k_1/k_2 > 1 + \sqrt{(1+\beta_i)}\sqrt{(1+\beta_j)}$ (6.7)

For $\beta_i > \beta_j$, $\Omega_i > \Omega_j$ requires $k_1/k_2 < 1 + \sqrt{(1+\beta_i)}\sqrt{(1+\beta_j)}$

Using these inequalities it can now be shown that, for $\beta_1>\beta_2>\ldots$,

$$\Omega_j = \min(\Omega_1, \Omega_2, \Omega_3\ldots) \quad \text{iff} \quad 1+\sqrt{(1+\beta_j)}\sqrt{(1+\beta_{j+1})} < k_1/k_2 < 1+\sqrt{(1+\beta_j)}\sqrt{(1+\beta_{j-1})}. \quad (6.8)$$

Conversely, for k_1/k_2 in the given range, the stability constraint equation on η is $1/\eta < \Omega_j$.

We here illustrate how this works for the case n=6. The θ's are given by (2/6)(π,2π) yielding β's (1/2, -1/2), corresponding to the factorization $\xi^6 - \eta^6 = (\xi^2 - \eta^2)(\xi^2+\xi\eta+\eta^2)(\xi^2-\xi\eta+\eta^2)$ and Ω's $\Omega_1 = (k_1/k_2 + 1/2)^2/(3/2)$, $\Omega_2 = (k_1/k_2 - 1/2)^2/(1/2)$. The RH analysis for n=6 also requires

$(k_1/k_2-1)>0$. To complete the n=6 example, define $[i,j] = 1 + \sqrt{(1+\beta_i)}\sqrt{(1+\beta_j)}$ and obtain [1,2] = 1.866. It then follows that for $k_1/k_2 > [1,2]$ we require $1/\eta < \Omega_1$ and for $1< k_1/k_2 < [1,2]$ we use $1/\eta < \Omega_2$. Using the conservation constraint $\sum = 6\,[k_3/k_2+a^*(1+k_1/k_2)]$ we determine the constraint on k_3/k_2 for the appropriate $1/\eta < \Omega_{min}$ (see Eq.(7.1) below) and then deduce the corresponding a*. The steady-state value y* follows and the case n=6 can be considered fully solved.

7. *Summary of analysis for the general n=n case, LV(3,n)*

The steady-state FP is $x_i \rightarrow k_3/k_2$, $y_i \rightarrow k_1a^*/k_2$, $a_i \rightarrow a^* = [\sum/n - k_3/k_2]/(1+k_1/k_2)$

from conservation, $1/\eta < \Omega_{min}$ from RH analysis, in which the θ's are given by $\theta = (2/n)(\pi,2\pi,3\pi,\ldots(n-2)\pi/2)$ for n even and $\theta = (2/n)(\pi,2\pi,3\pi,\ldots(n-1)\pi/2)$ for n odd. Ω_{min} is obtained using $k_1/k_2 > [1,2] \rightarrow \Omega_{min} = \Omega_1$; $[1,2]> k_1/k_2 > [2,3] \rightarrow \Omega_{min} = \Omega_2$; …., $[i-1, i] > k_1/k_2 > [i,i+1] \rightarrow \Omega_{min} = \Omega_i$. For n odd we have the additional constraint $(k_1/k_2 + \beta_{min}) > 0$, and for n even $(k_1/k_2 – 1) > 0$

Finally, using $a^* = [\sum/n - k_3/k_2]/(1+k_1/k_2)$, $\eta = \frac{a^*{k_2}^2}{k_1k_3}$, and $1/\eta < \Omega_{min}$, the stability constraint on k_3/k_2 follows, viz

$$k_3/k_2 < (\sum/n)/[1+ (k_1/k_2)(1+ k_1/k_2)/ \Omega_{min}] \tag{7.1}$$

Then for chosen values of k_1/k_2 and k_3/k_2, the corresponding values of x*, a*, y* follow,

viz $x^* = k_3/k_2$, $a^* = [\sum/n - k_3/k_2]/(1+k_1/k_2)$, and $y^*=k_1a^*/k_2$, and the problem is solved.

Two final examples, n=7 and n=8 follow to clarify how the stability routine works.

For the case n=7: $7\theta/2 = (\pi, 2\pi, 3\pi) \rightarrow \beta_1 = \cos\theta_1 = 0.6235$, $\beta_2 = -0.2225$, $\beta_3 = -0.901$.

Then $[1,2] =1 +\sqrt{(1+\beta_1)}\sqrt{(1+\beta_2)} = 2.1235$, [2,3]=1.2775. Thus for $k_1/k_2 >2.1235$ we have $1/\eta < \Omega_1$, for $1.2775< k_1/k_2<2.1235$ we have $1/\eta < \Omega_2$, and for $0.901< k_1/k_2<1.2775$ we have $1/\eta < \Omega_3$ (note $0.901 = - \beta_{min}$, corresponding to $(k_1/k_2 + \beta_{min}) > 0$)

For the case n=8: $8\theta/2 = (\pi, 2\pi, 3\pi) \rightarrow \beta_1 = \cos\theta_1 = 1/\sqrt{2}$, $\beta_2 = 0$, $\beta_3 = -1/\sqrt{2}$.

Then $[1,2] =1 +\sqrt{(1+\beta_1)}\sqrt{(1+\beta_2)} = 2.306$, [2,3]=1.5412. Thus for $k_1/k_2 >2.306$ we have $1/\eta < \Omega_1$, for $1.5412< k_1/k_2<2.306$ we have $1/\eta < \Omega_2$, and for $1< k_1/k_2<1.5412$ we have $1/\eta < \Omega_3$. (note the $(k_1/k_2 - 1) > 0$, derived from the $(\xi^2-\eta^2)$ factor in Eq.6.2.)

In each case, the constraint on k_3/k_2 follows using Eq.(7.1) and the value of a*(and thus y*) follows from the conservation equation $\sum = n[k_3/k_2+a^*(1+k_1/k_2)]$.

The reader is encouraged to numerically solve the governing equations to verify the accuracy of the above stability routine.

Whither now?

The next obvious case to consider is that of *LV(4,n)*. As expected the Routh-Hurwitz analysis and determination of the stability constraints on the reaction constants $k_1,\ldots,k_4$ is correspondingly more complicated than for LV(3,n) and it turns out that, unlike the LV(3,n) described above, the constraints on LV(4,n) are hard to specify in closed form, but rather involve a *numerical iteration* stage, which can be performed using EXCEL. The results of that investigation will be reported in a subsequent paper.

References

Bodson, M. (2020). Explaining the Routh–Hurwitz criterion: A tutorial presentation [Focus on education]. *IEEE Control Systems Magazine, 40*(1), 45-51. https://doi.org/10.1109/MCS.2019.2949974

Chen, S., Shi, J., Shuai, Z., & Wu, Y. (2022). Global dynamics of a Lotka-Volterra competition patch model. *Nonlinearity, 35*, 817-842. https://doi.org/10.1088/1361-6544/ac3c2e

Feng, W., Rock, B., & Hinson, J. (2011). On a new model of two-patch predator-prey system with migration of both species. *Journal of Applied Analysis and Computation, 1*(2), 193-203. Retrieved from http://jaac-online.com/

Hethcote, H. W. (2000). The mathematics of infectious diseases. *SIAM Review, 42*(4), 599-653.

Hurwitz, A. (1895). Ueber die Bedingungen, unter welchen eine Gleichung nur Wurzeln mit negativen reellen Theilen besitzt. *Mathematische Annalen, 46*(2), 273-284. https://doi.org/10.1007/BF01446812

Kang, Y., Sasmal, S. K., & Messan, K. (2017). A two patch prey-predator model with predator dispersal driven by predation strength. *Mathematical Biosciences and Engineering, 14*(4), 843-880. https://doi.org/10.3934/mbe.2017046

Liu, W., Liu, J., & Chen, S. (2024). Dynamics of Lotka-Volterra competition patch models in stream with two branches. *Bulletin of Mathematical Biology, 86*(14). https://doi.org/10.1007/s11538-023-01243-3

Lotka, A. J. (1910). Contribution to the theory of periodic reaction. *The Journal of Physical Chemistry, 14*(3), 271-274. https://doi.org/10.1021/j150111a004

Lotka, A. J. (1920). Analytical note on certain rhythmic relations in organic systems. *Proceedings of the National Academy of Sciences of the United States of America, 6*(7), 410-415. https://doi.org/10.1073/pnas.6.7.410

Lotka, A. J. (1925). *Elements of physical biology*. Reprinted as *Elements of mathematical biology* by Dover in 1956.

Lyapunov, A. M. (1892). *The general problem of the stability of motion* [Doctoral dissertation, University of Kharkov, Kharkov, Russia]. English translations: (1) *Stability of motion* (Academic Press, New York & London, 1966); (2) *The general problem of the stability of motion* (A. T. Fuller, Trans.). Taylor & Francis, London, 1992.

Routh, E. J. (1877). *A treatise on the stability of a given state of motion: Particularly steady motion*. Macmillan.

Sun, G., & Mai, A. (2018). Stability analysis of a two-patch predator-prey model with two dispersal delays. *Advances in Difference Equations, 2018*(1), 373. https://doi.org/10.1186/s13662-018-1833-2

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature, 118*, 558-560.

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