1 2 predators competing for 1 prey

I consider here the equations for two predator species competing for 1 prey species. The equations of the system are

$$\begin{cases} H'(t) &= rH(1-\frac{H}{K}) - \frac{a_1 H P_1}{1+a_1 T_1 H} - \frac{a_2 H P_2}{1+a_2 T_2 H} \\ P_1'(t) &= \frac{\gamma_1 a_1 H P_1}{1+a_1 T_1 H} - d_1 P_1 \\ P_2'(t) &= \frac{\gamma_2 a_2 H P_2}{1+a_2 T_2 H} - d_2 P_2. \end{cases} \tag{1}$$

It follows the standard assumptions of a prey-predator: the prey species grows (in absence of predators) logistically, while predation rate of each species follows Holling's model (a_i is the attack coefficient and T_i is the time necessary for "handling" a prey); finally γ_i are the coefficients of conversion prey-predator, and d_i are the mortality rates of predators in absence of preys.

IIt can be found numerically that, for certain parameter values, it is possible to find positive periodic solution, i.e. the two predators coexisting with the prey along a limit cycle (see Figs. 1 and 3).

To (partially) understand the behaviour of the system and the existence of the periodic solution shown in figure, we start from the analysis of the local stability of the equilibrium points (and of some periodic solutions) of system (1). First of all, I make the system non-dimensional, using the same transformation used for the system with a single prey species[1]:

$$u = \frac{H}{K},\ v_1 = \frac{P_1}{\gamma_1 K},\ v_2 = \frac{P_2}{\gamma_2 K},\ \tau = d_1 t.$$

Using these transformations and setting $\dot{} = \frac{d}{d\tau}$, one obtains

$$\begin{cases} \dot{u}(t) &= \rho u(1-u) - \frac{\beta_1 u v_1}{1+\alpha_1 u} - \frac{\beta_2 u v_2}{1+\alpha_2 u} \\ \dot{v}_1(t) &= \frac{\beta_1 u v_1}{1+\alpha_1 u} - v_1 \\ \dot{v}_2(t) &= \frac{\beta_2 u v_2}{1+\alpha_2 u} - \delta v_2. \end{cases} \tag{2}$$

with

$$\rho = \frac{r}{d_1},\ \beta_1 = \frac{\gamma_1 a_1 K^2}{d_1},\ \beta_2 = \frac{\gamma_2 a_2 K^2}{d_1},\ \alpha_i = a_i T_i K,\ \delta = \frac{d_2}{d_1}.$$

The equilibria are those found analysing the system 1 prey- 1 predator:

$$E_0 = (1,0,0) \qquad E_1 = (u_1^*, \Psi_1(u_1^*), 0) \qquad E_2 = (u_2^*, 0, \Psi_2(u_2^*)) \tag{3}$$

where

$$u_1^* = \frac{1}{\beta_1 - \alpha_1} \quad \text{and} \quad u_2^* = \frac{\delta}{\beta_2 - \alpha_2 \delta}$$

[1] in this case, choosing $\tau = rt$ would yield a more symmetric system, but I stick to the same transformations

are the solutions of

$$\omega_1(u) = 1,\ \omega_2(u) = \delta, \quad \text{with } \omega_i(u) = \frac{\beta_i u}{1 + \alpha_i u}$$

and

$$\Psi_i(u) = \frac{\rho}{\beta_i}(1-u)(1+\alpha_i u).$$

In what follows, we will assume $\beta_1 > \alpha_1$ and $\beta_2 > \alpha_2\delta$, so that the expressions for u_i^* are positive. Moreover, for the equilibrium E_i to be in the positive half-plane it is necessary $1 > u_i^*$.

We remind that the equilibrium $(1, 0)$ is (globally) asymptotically stable for the system with 1 prey and the predator i if $1 < u_i^*$. The equilibrium $(u_i^*, \Psi_i(u_i^*))$ is (globally) asymptotically stable if $u_i^* < 1$ and $u_i^* > \hat{u}_i$ where $\hat{u}_i$ is the maximum point on $[0, 1])$ of $\Psi_i(u)$. In the specific case,the condition for the stability of E_1 is

$$\frac{\alpha_1 - 1}{2\alpha_i} < u_1^* < 1 \iff \alpha_1 + 1 < \beta_1 < \frac{\alpha_1(\alpha_1 + 1)}{\alpha_1 - 1}.$$

Finally, for $\beta_1 < \dfrac{\alpha_1(\alpha_1 + 1)}{\alpha_1 - 1}$ the system with 1 prey and the predator 1 has a periodic orbit (of period τ_1)

$$\Gamma_1 = \{(\bar{u}_1(t), \bar{v}_1(t)), t \in [0, \tau_1]\}$$

asimptoticaly stable, and globally attractive from the positive half-plane, with the exception of the equilibrium $(u_1^*, \Psi_1(u_1^*))$. An example of the periodic solution is shown in Fig. 1. Similar considerations hold for the system with prey and predator 2, except for the need to keep track of the constant δ.

Let us now consider if the system (2) has internal equilibrium points. Setting $\dot{v}_1$ equal to 0, we see that it must be (if $v_1 \neq 0$) $u = u_1^*$; setting $\dot{v}_2$ equal to 0, we see that it must be (if $v_2 \neq 0$) $u = u_2^*$. Assuming, generically $u_1^* \neq u_2^*$, it turns out that there are no internal equilibria, and all the equilibria are presented in (3).

In what follows, let us assume, without loss of generality, $u_1^* < u_2^*$. As u_i^* is the resource(=prey) level at which the population of predators i can maintain, the principle of survival of the competitor with the lowest level of necessary resource makes us think that only the predator 1 will survive, while the 2 predators will go extinct.

Let us now analyse the problem, starting from the local stability of equilibria. Letting J_i be the Jacobian of the system in E_i, we have

$$J_0 = \begin{pmatrix} -\rho & -\frac{\beta_1}{1+\alpha_1} & -\frac{\beta_2}{1+\alpha_2} \\ 0 & \omega_1(1) - 1 & 0 \\ 0 & 0 & \omega_2(1) - \delta \end{pmatrix} \qquad J_1 = \begin{pmatrix} \frac{u_1^*}{1+\alpha_1 u_1^*}\Psi'_1(u_1^*) & -\frac{\beta_1 u_1^*}{1+\alpha_1 u_1^*} & -\frac{\beta_2 u_1^*}{1+\alpha_2 u_1^*} \\ \frac{\beta_1 v_1^*}{(1+a_1 u_1^*)^2} & 0 & 0 \\ 0 & 0 & \omega_2(u_1^*) - \delta \end{pmatrix}$$

and J_2 analogous to J_1 exchanging 1 with 2, and vice versa.

J_0 is triangular; hence its eigenvalues are the elements on the diagonal: the first $(-\rho)$ is certainly negative, while $\omega_1(K) - 1 < 0$ if and only if $1 < u_1^*$ (remember that ω_i is an increasing function and u_1^* is the solution of $\omega_1(u) = 1$); similarly $\omega_2(1) - \delta$ if and only if $1 < u_2^*$. Thus E_0 is asymptotically stable if

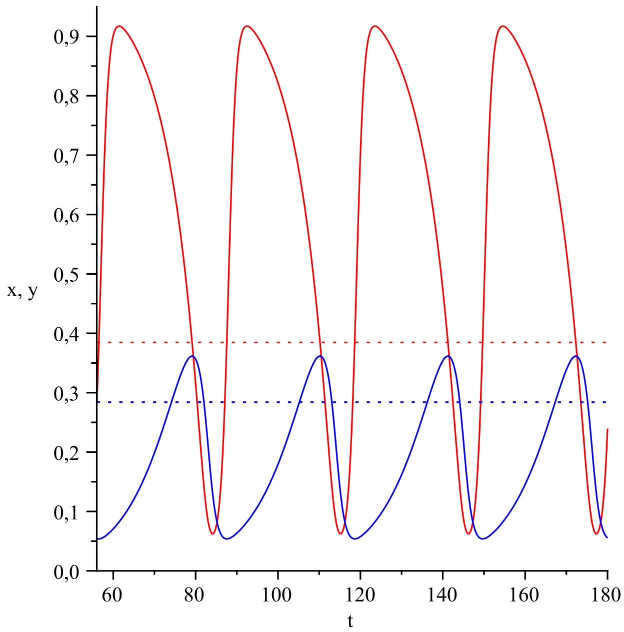

Figure 1: The values of $u(t)$ (red) and $v_1(t)$ (blue) over a periodic orbit. Parameter values are $r = 1.2$, $K = 1$, $\lambda_1 = 15.6$, $d_1 = 1$, $\alpha_1 = 13$. The horizontal lines denote the values of the (unstable) equilibrium (u_1^*, v_1^*); it can be seen that $u(t)$ is more often above u_1^* than below, while the opposite holds for $v(t)$.

$1 < u_1^* < u_2^*$ (and then, the equilibria E_1 and E_2 are non-positive) and is unstable if $1 > u_1^*$.

J_1 is block- triangular; hence its eigenvalues are $\omega_2(u_1^*) - \delta$ and the eigenvalues of the top-left 2×2 matrix :

$$J_{11} = \begin{pmatrix} \frac{u_1^*}{1+\alpha_1 u_1^*}\Psi_1'(u_1^*) & -\frac{\beta_1 u_1^*}{1+\alpha_1 u_1^*} \\ \frac{\beta_1 v_1^*}{(1+a_1 u_1^*)^2} & 0 \end{pmatrix}.$$

J_{11} is the Jacobian matrix in (u_1^*, v_1^*) of the system with prey and predator 1 only; we know that it has both eigenvalues with negative real part if and only if

$$\alpha_1 + 1 < \beta_1 < \frac{\alpha_1(\alpha_1 + 1)}{\alpha_1 - 1}. \tag{4}$$

The third eigenvalue $(\omega_2(u_1^*) - \delta)$ is instead always negative under the assumption $u_1^* < u_2^*$. In fact ω_2 is increasing; thus $\omega_2(u_1^*) < \omega_2(u_2^*) = \delta$.

In conclusion, all eigenvalues di J_1 have negative real part, and so E_1 is asymptotically stable, if and only if condition (4) holds.

Moving to J_2, we can use the same arguments. An eigenvalue is $\omega_1(u_2^*) - 1$, always positive under the assumption $u_1^* < u_2^*$. The other two are the eigenvalues of J_{21}, top-left submatrix of J_2; these have negative real part under the condition

$$\delta(\alpha_2 + 1) < \beta_2 < \frac{\alpha_2 \delta(\alpha_2 + 1)}{\alpha_2 - 1}.$$

In any case, the equilibrium E_2 is unstable.

We have seen that, when $\beta_1 > \dfrac{\alpha_1(\alpha_1+1)}{\alpha_1 - 1}$, the system with prey and predator 1 only has a periodic orbit Γ_1 which is asymptotically stable. Γ_1 will be a periodic orbit also for the system (2); we may ask whether it will be asymptotically stable also for this.

Linearization can be used also for the analysis of the stability of periodic orbits, but is somewhat delicate. Proceeding formally, assume that $\bar{x}(t)$ is a periodic solution (of period T) (its values make the periodic orbit Γ) of the autonomous system $x'(t) = f(x(t))$. Let $u(t) = x(t) - \bar{x}(t)$ (the deviation, assumed to be small when studying the stability, from the periodic solution) and take its derivative. We obtain

$$u'(t) = f(x(t)) - f(\bar{x}(t)) = f'(\bar{x}(t))u(t) + o(u(t)) \approx f'(\bar{x}(t))u(t).$$

The linearized equation for the deviation is then

$$u'(t) = A(t)u(t) \quad \text{with} \quad A(t) = f'(\bar{x}(t)). \tag{5}$$

$A(t)$ is an $n \times n$ T-periodic matrix.

It can be shown (this is known as Floquet theory) that the fundamental solutions[2] $X(t)$ of (5) can be written in the form

$$X(t) = Z(t)e^{tR} \quad \text{with } Z(t+T) = Z(t).$$

It then follows that the asymptotic behaviour of the solutions of (5) is determined by the eigenvalues of e^{TR}. By linearisation, this determines also the stability of Γ.

The eigenvalues $\lambda_1, \dots, \lambda_n$ of e^{TR} are known as Floquet's multipliers. It can be proved that one of them (say λ_n) is equal to 1, because, if one considers a starting point deviating from $\bar{x}(0)$ in the direction of Γ, the solution from it will run again the same orbit Γ. The linearization theorem states that if $|\lambda_1|, \dots, |\lambda_{n-1}| < 1$, then the periodic orbit Γ is asymptotically stable; if at least one eigenvalue λ_i, $i = 1 \dots n-1$ satisfies $|\lambda_i| > 1$, then the periodic orbit Γ is unstable[3]. Unfortunately, it is generally impossible to obtain analytic expressions for the Floquet multipliers, or any sufficiente condition for them to be less than 1 in module.

In the specific case of system (1), it is instead possible to make some explicit computations. Without discussing explicitly Floquet theory, I simply look for solutions of (5) in the specific case. I limit myself to the third equation that becomes

$$u_3'(t) = u_3(t)\left(\frac{\beta_2 \bar{u}(t)}{1+\alpha_2 \bar{u}(t)} - \delta\right) \tag{6}$$

where $\bar{u}(t)$ refers to the values of u through the periodic orbit Γ_1 on the (u, v_1) plane.

The solution of (6) is

$$u_3(t) = u_3(0) \exp\left\{\int_0^t \left(\frac{\beta_2 \bar{u}(s)}{1+\alpha_2 \bar{u}(s)} - \delta\right) ds\right\}.$$

[2] i.e. a matrix such that its columns are independent solutions of the equation

[3] alternatively, $\lambda_1, \dots, \lambda_{n-1}$ can be obtained as the eigenvalues of the linearization of the Poincaré's map in an arbitrary point of the periodic orbit.

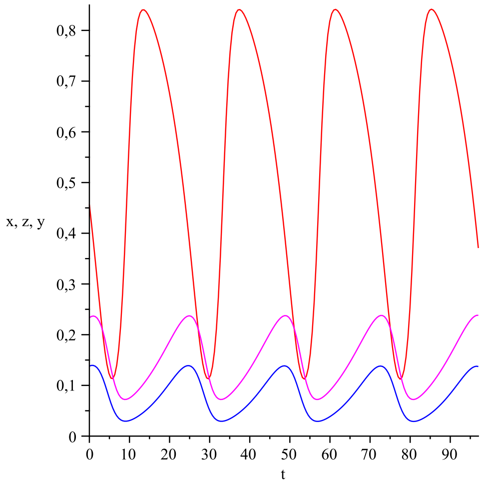

Figure 2: A periodic solution of the model (2); the red curve represents $u(t)$, the magenta $v_1(t)$ and the blue one $v_2(t)$. Parameter values are $\rho = 1.2$, $\beta_1 = 15.6$, $\beta_2 = 8.925$, $\alpha_1 = 13$, $\alpha_2 = 7.436$, $\delta = 0.9$.

It is easy to see that the asymptotic behaviour of $u_3(t)$ is the same as that of e^{zt} with

$$z = \frac{1}{T}\int_0^T \left(\frac{\beta_2 \bar{u}(s)}{1 + \alpha_2 \bar{u}(s)} - \delta \right) ds. \tag{7}$$

In other words, one Floquet multiplier is e^{zT}.

If $z > 0$, Γ_1 is then unstable. On the other hand, if $z < 0$, one has to look at the other Floquet multiplier (beyond 1). This can be found by looking at the first two equations. Without performing any computation (that anyway is very difficult), one can note that these will be the same equations that would be obtained by looking at the stability of Γ_1 for the 2-dimensional system with only the prey and predator 1.

As I have already stated, the periodic orbit Γ_1 for the 2-dimensional system with only the prey and predator 1is always asymptotically stable when it exists. Hence, its Floquet multipliers are 1 and another one smaller than 1 in module.

Summarizing, we have obtained that the periodic orbit Γ_1 is asymptotically stable for system (1) if $z < 0$ (z defined in (7)) and is unstable if $z > 0$.

One may wonder whether it is possible that $z > 0$ under the assumption $u_1* < u_2^*$. In fact, $\bar{u}(s)$ will fluctuate around u_1^* and, if one susbstitutes $\bar{u}(t) \equiv u_1^*$ in (7), one would obtain

$$\tilde{z} = \frac{1}{T}\int_0^T t \left(\frac{\beta_2 u_1^*}{1 + \alpha_2 u_1^*} - \delta \right) ds = \frac{\beta_2 u_1^*}{1 + \alpha_2 u_1^*} - \delta < \frac{\beta_2 u_2^*}{1 + \alpha_2 u_2^*} - \delta = 0 \tag{8}$$

by the definition of u_2^*,

The fact is, however, that $\bar{u}(t)$, while fluctuating around u_1^*, is more often above it than below it (see an illustration in Fig. 1) so that the value of z will generally be higher than $\tilde{z}$.

To make this argument precise, first note, by integrating $\frac{d}{dt}\log(v_1(t))$ from

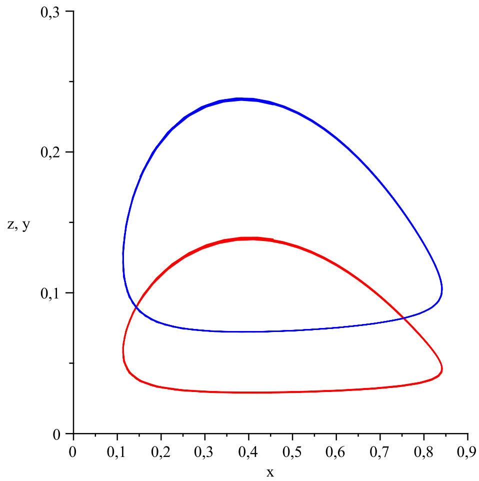

Figure 3: The periodic solution of the model (2) of Figure 1 in the phase planes (u, v_i). The blue curve represents (u, v_1), the red one (u, v_2)

0 to T, that over the periodic orbit Γ_1 necessarily holds

$$\frac{1}{T}\int_0^T \frac{\beta_1 \bar{u}(s)}{1+\alpha_1 \bar{u}(s)} = 1.$$

Using the functions $\omega_i(u(\cdot))$, this can be written as $\langle \omega_1(u) \rangle = 1$ where by $\langle \cdot \rangle$ we mean the average of a function over a period. Now $\omega_2(u)$ can be written as $G(x) := \omega_2(\omega_1^{-1}(x))$ with $x = \omega_1(u)$.

By inverting explictly ω_1, one computes

$$G(x) = \frac{\beta_2 x}{\beta_1 + x(\alpha_2 - \alpha_1)}, \text{ so that } G''(x) = \frac{\beta_2(\alpha_1 - \alpha_2)}{(\beta_1 + x(\alpha_2 - \alpha_1))^2}.$$

Hence, if $\alpha_1 > \alpha_2$, G is a convex function.

By Jensen's inequality, if $\alpha_1 > \alpha_2$,

$$\langle G(x) \rangle > G(\langle x \rangle) = G(1) = \omega_2(u_1^*).$$

In other words, while $\omega_2(u_1^*) < \omega_2(u_2^*) = \delta$, also the quantity used in (7) $\langle \omega_2(u) \rangle = \langle G(x) \rangle$ is greater than $\omega_2(u_1^*)$, so that it may be possible that $\langle \omega_2(u) \rangle > \delta$, i.e. $z > 0$. The numerical example in Figures 1 and 3 shows that indeed this is possible.

On the other hand, if $\alpha_1 \leq \alpha_2$, Jensen's inequality in the opposite direction shows that $z < 0$.

Hence, having chosen $u_1^* < u_2^*$, $\alpha_1 > \alpha_2$ together with $\beta_1 > \dfrac{\alpha_1(\alpha_1+1)}{\alpha_1 - 1}$, is a necessary condition for the instability of all boundary attractors. It still does not guarantee that $z > 0$, but, trying parameters carefully, one can obtain that. When all boundary attractors are unstable, then it appears that an internal periodic solution exists. Note that the system is not persistent, according to the definition given in a previous Section, since initial points in the (one-dimensional) stable manifold (which intersects the positive orthant) of E_1 will be attracted to E_1.