PARADOXES OF VULNERABILITY TO PREDATION IN BIOLOGICAL DYNAMICS AND MEDIATE VERSUS IMMEDIATE CAUSALITY

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Abstract. The causality scheme of an (essentially non symmetric) predator-prey system involves automatically advantages and disadvantages highly dependent on time. We study systems with one predator and one or two preys furnishing issues which involve mediate and immediate causality (naturally associated with the attractor and the previous transient). The issues are highly dependent on the parameter accounting for the vulnerability of the preys. When the vulnerability is small, an increase of it implies a (demographic) disadvantage for the preys, but, when it is large (involving periodic cycles) an increase turns out in an advantage because of the rarefaction of predators (this is associated with average populations on the periodic cycles). When two preys with different vulnerability are present, the most vulnerable may disappear (i.e. the attractor does not contain such prey). This phenomenon only occurs when the less vulnerable prey is nevertheless able to support the predator; otherwise, this one keeps eating anyway the other preys. The mechanism of such patterns are better described in terms of attractors and stability than in terms of advantages versus disadvantages (which are drastically dependent on the viewpoints of the three species).

1. Introduction. In ecological dynamics, the causal structure of predator-prey systems is rather entangled and impossible to describe in terms of an elementary “survival of best adapted”. Not only the predator-prey relation cannot be described in terms of “better and worse”, but a rapid examination of the causal elements involved sends naturaly to the consideration of immediate and mediate advantages and disadvantages. The time, with short and long terms is naturally involved. Indeed, the preys may obviously live alone, and their consumption by a predator always constitute a demographic disadvantage for the preys. Oppositely, the same process is a clear advantage for the predators, which allows them not to die of hunger in the near future, but if the consumption is immmoderate, it may lead to a decrease of the prey population, which constitutes a disadvantage for the same predators. That is the key point of the predator-prey system, which is at the origine of periodic cycles which appear in certain cases. Obviously, the theory of dynamical systems is naturally involved, and causality is often better described in terms of stability and attractors than by advantages and disadvantages (see also [6]).

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This paper is written in the general framework of population dynamics. So, \( x, y \) (or \( x(t), y(t) \)) denote the number of individuals (measured with some unity) of the corresponding species, but we often write “the species \( x \) or \( y \)”. Moreover, it is understood that the predators eat preys (and nothing else) according to an explicit process, whereas the preys live on their own subsistences (which are more or less taken into account by implicit “logistic terms” involving equilibrium populations).

This is not a genuine mathematical paper, but rather a computing one. Mathematics are practically reduced to description and comments on the basis of the numerical examples (done with Mathematica). We did not search to generalize the examples, nor to give an exhaustive description of the domains in the space of parameters leading to the various phenomena presented here. Our aim is only concerned with the description of very simple examples in low dimension (2 or 3) exhibiting the phenomena and the corresponding causal mechanisms. In any case, it is worthwhile recalling a classical citation of Stephen Smale (in [9]): “It is shown that the ODE used to describe competing species are compatible with any dynamical behavior provided the number of species is very large”. It should be noted that in low dimension many striking patterns may occur, including for instance chaos ([3]), burst oscillations ([10]) and entangled transients ([4]). Our purpose here is to exhibit explicit examples in low dimension. It should be emphasized that the term “paradox” is mainly used in order to bring attention on remarkable facts, while their causality is always explained (but the attentive reader will certainly find in this paper open questions than answers).

The main parameter we deal with is the vulnerability of the predation. Roughly speaking, it may be defined as the proportionality factor between the effective consumption of preys and the number of encounters of preys and predators (by unit of time). When coupled with a satiety threshold (i.e. the so-called Holling type II predation function), vulnerability is the key parameter giving either a parsimonious or violent process, which lead respectively to an equilibrium state or a periodic (intrinsic) oscillation. But most interesting phenomena are concerned with two preys with different vulnerability, which implies clear advantages of one of them on the other, whereas this advantage is most effective in the situation of a drastic predation.

The paper is organized as follows:

In Section 2 we give the basic model for one predator and one prey.

In section 3 we describe the various patterns according to the vulnerability.

Section 4 is devoted to computations on the periodic solutions, mainly the average values of the populations on a period and their dependence on the vulnerability. It appears that the average populations are not monotone functions of the vulnerability (there are reversals of the basic trends for sufficiently large vulnerability).

The model for one predator and two preys is given in Section 5.

In Section 6 we display computations for different vulnerabilities of the two preys. We exhibit cases of exclusion of one of the preys which are again non monotone with respect to the vulnerabilities. Certain patterns may be described in terms of mediate versus immediate causality.

A punctual example of vulnerability depending on time by a given periodic function with large period is displayed in section 7. It exhibits some kind of burst oscillations.

Section 8 contain some conclusions and comments.
2. The basic predator - prey model. In this section, we consider the system for the joint evolution of a prey population $x(t)$ and a predator population $z(t)$,

$$
\begin{align*}
\dot{x} &= ax(1 - x/p) - z \tanh(vx) \\
\dot{z} &= z(-c + \tanh(vx))
\end{align*}
$$

We note that, in the absence of predators $z$, the equation for the population of the preys $x$ is a classical logistic equation were $a$ denote the natural population growth with abundant ressources, and $p$ is the equilibrium population with the ressoures of their habiitat. Equivalently, in the absence of preys, the population of predators $z(t)$ has a natural population decrasing $c$.

The “predation function” $\tanh(vx)$ denotes the number of preys consumed by unit of time by each predator. This function is obviously equal to $vx(t)$ for small $x$, whereas it has an horizontal asymptotics equal to 1, which denotes the upper bound of saciety of the predators when the preys are abundant. It is worthwhile noticing that this predation function (which enters clearly in the so-called Holling type II) is essentially analogous to the widely used $vx/(vx+1)$ (see for instance [7]; [10]) which enjoys the same above mentioned patterns for small and large values of $x$. The two functions are jointly plotted in Fig 1; it is apparent that our function aproaches much more the heuristic scheme accounting for the fact that the predation is proportional to the randomly encountered prays $x$ (with proportionality factor $v$), replaced by the saciety level for sufficiently abundant preys. So, this model is closer of the heuristics than the classical one, allowing a better understanding of the various phenomena.

It should be noted that the previous model is general, even if some parameters are apparently taken with special values. Indeed, the saciety level is taken to be equal to 1; this is general, provided the unit for counting the preys is taken equal to that saciety level. Analogously, the term $z \tanh(vx)$ is the same in the two equations; this amounts to saying that the consumed prays are automatically transformed in predators, whereas there is an obvious transformation factor. In order to have it equal to 1 it is sufficient to fix the unit for counting the predators equal to the transformed quantity of the preys unit.

The classical very idealized Lotka - Volterra model (see for instance [7], [2], [5], [1]) corresponds to the saciety level as well as the equilibrium population equal to $+\infty$. It gives orbits which are all cycles (periodic solutions) which obviously corresponds to an “indifferent stability” which may become either stable or unstable.
under small perturbations; so, this model is not structurally stable. Later, A. Kolmogorov (see for instance [8]) gave sufficient conditions on the predation function and other parameters for getting a stable cycle, which is classically structurally stable). Modern models, including ours, incorporate two differences: a finite (instead of infinite) equilibrium population of preys (which constitutes a clear disadvantage for them) and a satiety limit of the predation function, which may be considered as a disadvantage for the predators. As a consequence, we are in presence of a trade-off situation which is highly dependent on the numerical values of the various parameters. As a matter of fact, there are three main possibilities exhibiting a stable cycle (Figure 2), a stable foyer equilibrium (Figure 3) and a node stable equilibrium (figure 4). The values of the parameters are \( a = 1, p = 4, c = 0.7616, v = 0.85 \) in Fig 2, \( v = 0.6 \) in Fig 3, \( v = 0.35 \) in Fig 4. Note that we often take \( c = 0.7616 \) in numerical computations; this amounts to \( c = \text{Tanh}(1) \), which is useful for certain verifications. Moreover, this value of \( c \) is somewhat far from 0 and 1, ensuring a good compromise between the extreme admissible values of \( c \) (see the last equation (1)).

3. Dependence of the main features on the vulnerability \( v \). The purpose of this section is to study the nature of the solution pattern as a function of the vulnerability parameter \( v \). Most of the properties are easier to prove for a slightly more general system, where \( ax(1 - x/p) \) is replaced by a smooth function \( f(x) \) with decreasing derivative, vanishing for \( x = 0 \) and some positive value \( p \) and \( \text{Tanh}(vx) \) is replaced by a smooth growing function \( \varphi(vx) \) with decreasing derivative, taking the value 0 at \( vx = 0 \) and tending asymptotically to 1 for \( vx \to +\infty \), namely:

\[
\begin{align*}
\dot{x} &= f(x) - z\varphi(vx) \\
\dot{z} &= z(-c + \varphi(vx))
\end{align*}
\]

The first important element is the equilibrium point (coordinates \( x_0 > 0, z_0 > 0 \)), given by:
Figure 3. Typical pattern of predation (stable foyer case). System (1), values of the parameters \( a = 1, p = 4, c = 0.7616, v = 0.6 \).

Figure 4. Typical pattern of predation (stable node case). System (1), values of the parameters \( a = 1, p = 4, c = 0.7616, v = 0.35 \).

\[
\begin{align*}
0 &= f(x_0) - z_0\varphi(vx_0) \\
0 &= -c + \varphi(vx_0)
\end{align*}
\]

so that the equilibrium is:

\[
\begin{align*}
x_0 &= \varphi^{-1}(c)/v \\
z_0 &= f(x_0)/c
\end{align*}
\]

where \( \varphi^{-1} \) denotes the inverse function of \( \varphi \). It is easily seen that, for very small \( v \), \( \varphi(vp) < c \) which implies \( \dot{z} < 0 \) at \( x = p \), the equilibrium of the \( x \) alone. The predation is not viable, as it cannot balance the natural mortality of the predators.
For $v$ larger than the value giving $\varphi(vp) = c$, there is an equilibrium point with $z_0 > 0$ according to the first equation (4). For $v$ varying between the viability threshold and $+\infty$, the equilibrium point describes a parabola (in the case of $Tanh$, or in general a curve which is the graph of the function $f(x)/c$).

This equilibrium may be, as we shall see in the sequel, either stable or unstable, node or focus. But in any case, it enjoys an interesting property following from the very phenomenon of predation. Considering the lines parallel to the coordinate axes passing by the equilibrium, it is easily seen that the orbits cut these lines with the counter-clock-wise orientation as $t$ increases. Indeed, on the points on the right of the equilibrium, the number of predators is the same as in the equilibrium, whereas the number of preys is larger than at equilibrium, so that the population of predators grows and the line is cut upwards. Obviously, the opposite holds at points on the left of the equilibrium. Moreover, at points $(x_0, y)$ with $y > y_0$, the number of preys is the same as in the equilibrium, whereas the number of predators is larger than at equilibrium, so that the population of preys decreases and the line is cut from right to left, and the opposite for $y < y_0$.

Let us now consider the nature of the equilibrium and its stability. They are given by the jacobian matrix at the equilibrium $(x_0, y_0)$

$$J_0 = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

with

\[
\begin{align*}
a_{11} &= f'(x_0) - z_0 v \varphi'(vx_0) \\
a_{12} &= \varphi(vx_0) = c \\
a_{21} &= z_0 v \varphi'(vx_0) \\
a_{22} &= -c + \varphi(vx_0) = 0
\end{align*}
\]

The corresponding eigenvalue equation is:

$$\lambda^2 - a_{11} \lambda - a_{12} a_{21} = 0$$

The main feature is the PAH bifurcation (for Poincaré, Andronov, Hopf), accounting for the exchange stability/unstability of the equilibrium. It appears when $Div_0 = 0$, where $Div_0$ denotes the divergence of the vector field at $(x_0, y_0)$; it is also the trace of the jacobian matrix $a_{11} + a_{22}$. On account of (6) $a_{22} = 0$ so that

$$Div_0 = f'(x_0) - z_0 v \varphi'(vx_0)$$

This expression is clearly negative when $f'(x_0) < 0$ and consequently the equilibrium is a stable focus in this region. Moreover, when $v \not\to \infty$ (i.e. $x_0 \not\to 0$), there is necessarily a bifurcation and the equilibrium becomes an unstable focus. Indeed, developing for small $x$ we have $f(x_0) \simeq f'(0)x_0 = f'(0)\varphi^{-1}(c)/v$, and multiplying and dividing the last term of (8) by $x_0$ and on account of

$$z_0/x_0 = f(x_0)/(cx_0) \simeq f'(0)/c$$

we get

$$Div_0 = f'(0)[1 - \varphi'(vx_0)x_0/c] = f'(0)[1 - \varphi'(vx_0)\varphi^{-1}(c)/c]$$

Moreover, as $\varphi$ is a growing function with decreasing derivative taking the values 0 and $c$ at 0 and $\varphi^{-1}(c)$ respectively, we have necessarily

$$\varphi'(vx_0) = \varphi'((\varphi^{-1}(c)) < c/\varphi^{-1}(c)$$

so that the expression (10) is necessarily positive for small $x_0$. This proves the presence of an intermediate bifurcation.
Moreover, at the bifurcation, \( a_{11} = 0 \) (and always \( a_{22} = 0 \)) so that the discriminant of the eigenvalue equation is \(-4a_{12}a_{21}\), then negative according to (6), so that the eigenvalues are imaginary in the vicinity of the bifurcation, which is a PAH one. As a consequence, for \( v \) slightly smaller than this PAH bifurcation, the equilibrium is a stable focus.

Otherwise, it is easily seen that there is another bifurcation passing from stable node for small \( v \) to stable focus in the vicinity of the PAH bifurcation. Indeed, according to the above considerations, the eigenvalues are imaginary in the vicinity of the PAH bifurcation, whereas for \( v \) equal to the viability threshold (i.e. when \( x_0 = p, y_0 = 0 \)) the two eigenvalues are: one strictly negative and the other equal to 0 (corresponding respectively to the horizontal and transversal eigenvectors). This proves that there is an intermediate transition from real to imaginary eigenvalues, i.e. from stable node for small \( v \) to stable focus nearby the PAH bifurcation.

4. Computing the periodic solutions and their mean values. First paradoxes. Most of the explanations in this section should be read looking at figure 5.

Before computing the stable cycles, it is worthwhile describing on a figure the main features of the previous section. We fix in system (1) the parameters \( a = 1, p = 4, c = 0.7616 \) (which are well representative values) and we take the vulnerability \( v \) varying between 0 and \(+\infty\). According to (2) and (3), the equilibrium point \((x_0(v), y_0(v))\) as a function of \( v \) derives the parabola in Figure 5. For \( v < 0.25 \) the predation is not viable; for \( v = 0.25 \) the equilibrium is that of the preys themselves, i.e. \((4, 0)\) then, for increasing values of \( v \), the equilibrium follows the parabole up to its apex, which corresponds to \( v = 0.5 \) and goes dawn along the parabola towards the origin, which is the limit for \( v \nearrow +\infty \). The PAH bifurcation takes place at \( v \approx 0.78 \), (between the apex and the origin, according to the theory in the previous section). For larger values of \( v \) the equilibrium is unstable, so that it is no longer an attractor.

The shape of this curve is quite natural for \( 0.25 < v < 0.5 \); Indeed, as the vulnerability increases the equilibrium populations of preys and predators are respectively decreasing and increasing. But, for \( v \) between the apex and the PAH bifurcation, i.e. \( 0.5 < v < 0.78 \), the shape is a little paradoxical, as the increase of the vulnerability implies decreasing of the populations of both preys and predators. The explanation of such situation is obviously that the rarefaction of the preys implies damage for the predators.

We next describe the stable cycles which replace as attractors the equilibria for \( v \) larger than the PAH bifurcation, say \( 0.78 < v < +\infty \). This description obviously relies on numerical computations (easily obtained with Mathematica). The PAH bifurcation obviously starts by replacing as attractor the equilibrium by a small (stable) cycle surrounding the (unstable) equilibrium. For increasing \( v \), the equilibrium point goes along the parabola towards the origin, whereas the corresponding surrounding cycle expands. At the limit \( v \nearrow +\infty \), the cycle becomes some sort of curvilinear triangle with two vertices tending to the equilibria \((0, 0)\) and \((p, 0)\) and another one on the axis \( x = 0 \) (which is not an equilibrium). The picture of the cycles with very high \( v \) is easy to understand: the predation is drastic and fast, so that, starting nearby the the equilibrium of the preys \((p, 0)\), there is a rapid consumption of preys and growing of the predators population; this leads to an almost-extinction of the preys (somewhere near the axis \( x = 0 \)) which implies a
fall of the population of predators (the point goes to the origin); but, when both populations are small, the preys are not consumed and their population grows again, going towards the equilibrium \((p,0)\), thus closing the cycle.

For the values \(0.78 < v < +\infty\) corresponding to stable cycles, the internal (unstable) equilibrium is not very significant; it is most worthwhile computing the average values of \(x(t)\) and \(z(t)\) on the period of the cycle, which amounts to the effective (time averaged) populations. As well as the cycles themselves, the average values can only be computed, there is no rigorous mathematical theory concerning their values and their evolution as functions of the vulnerability \(v\). These points are marked on figure 5 for \(v = 0.85, v = 1, v = 1.25\) and \(v = 6\) (as well as the corresponding unstable equilibria on the parabola).

The main feature of the curve of these averages is that, instead of going towards the origin for increasing \(v\) (as the unstable equilibria do), the averages have increasing \(x\) and decreasing \(z\). The limit position for \(v \to +\infty\) is impossible to compute, as the period itself tends to \(\infty\). The computed average values \((\overline{x(v)}, \overline{z(v)})\) are:

\[
\begin{align*}
(\overline{x(0.85)}, \overline{z(0.85)}) &= (1.30, 1.08) \\
(\overline{x(1.0)}, \overline{z(1.0)}) &= (1.53, 0.94) \\
(\overline{x(1.25)}, \overline{z(1.25)}) &= (1.78, 0.79) \\
(\overline{x(6.0)}, \overline{z(6.0)}) &= (2.21, 0.50)
\end{align*}
\] (12)

The fact that for very large values of \(v\) the average value \(\overline{x(v)}\) increases with \(v\) may be easily explained on the basis of the above description (see also figure 5). Indeed, as \(v \to +\infty\), the cycle becomes a curvilinear triangle with two vertices nearby the equilibria \((0,0)\) and \((p,0)\); the speed along the orbit is very slow at the portions neigbouring that two equilibria, so that these portions account for the main part of the average; it is natural that the averages tend towards some compromise between them instead of going to the one of them (the origin, as the unstable equilibria do).

It is nevertheless worthwhile noting a new paradox: according to (12), for large \(v\), \(x(v)\) (resp. \(z(v)\)) increases (resp. decreases) with \(v\), which is exactly the opposite
to the behavior of $x_0(v)$ and $z_0(v)$ for small $v$. This accounts for the foreseen fact that a very strong predation turns out in a disadvantage for the predators.

5. **Two preys and a predator.** The previous model may be easily generalized to the case of two preys $x$ and $y$. Denoting by $u$ and $v$ the respective vulnerabilities, when $x$ and $y$ are small, each predator consumes them according to the encountered individuals, but the satiety appears when the total consumption (by unit of time) reaches its threshold. This gives

$$Tanh(ux + vy)$$

(13)

This is the total consumption by unit of time and of predator. The parts of $x$ and $y$ are proportional to the encountered individuals, but the satiety appears when the total consumption (by unit of time) reaches its threshold. This gives

$$\tanh (ux + vy) \frac{ux}{ux + vy}$$

(14)

and

$$\tanh (ux + vy) \frac{vy}{ux + vy}.$$  

(15)

It is apparent that function (14) evolves from $vx$ for small $vx$ to 1 for large $vx$. (14) behaves analogously.

This gives the system:

$$\begin{align*}
\dot{x} &= ax (1 - (x + \delta y)/p) \\
\dot{y} &= by (1 - (y + \delta x)/q) \\
\dot{z} &= z (-c + tanh (ux + vy))
\end{align*}$$

(16)

Here $p$ and $q$ are respectively the equilibrium populations of $x$ and $y$ in the absence of the other two species, and $\delta$ denotes a parameter describing the independence of the two preys $x$ and $y$ with respect to their subsistences: $\delta = 0$ when the two preys are absolutely independent (rabbits and truts, say) and $\delta = 1$ when they are exchangeable with respect to their subsistences (two races of rabbits).

Numerical examples of solutions of this system will be given in the next section.

Clearly, $x = 0$ and $y = 0$ are invariant manifolds of system (16) corresponding to the absence of one or the other preys. For an ultior study of stability, it is worthwhile considering the system for $x = 0$:

$$\begin{align*}
\dot{y} &= by (1 - y/q) - z \tanh (vy) \\
\dot{z} &= z (-c + \tanh (vy))
\end{align*}$$

(17)

The corresponding equilibrium $(0, y_0, z_0)$ is given by

$$\begin{align*}
Tanh(vy_0) &= c \\
z_0 &= by_0 (1 - y_0/q) / c.
\end{align*}$$

(18)

The transversal stability (i. e. with respect to a small perturbation of $x$) of such equilibria is given by the corresponding variation equation for small $x$ (linearization of (16) for small $x$) i.e.:

$$\frac{\dot{x}}{x} = a (1 - \delta y_0/p) - z_0 \tanh (vy_0) \frac{u}{vy_0}$$

(19)

and writing it according to (18) in terms of the variable $y_0$:

$$\frac{\dot{x}}{x} = a (1 - \delta y_0/p) - \frac{bu}{Tanh^{-1}(c)} y_0 (1 - y_0/q)$$

(20)
The graph of this function of \( y_0 \) is easy to understand on account of the various parameters. The first term is a straight line, which is either horizontal (i.e., a constant function) when \( \delta = 0 \) or decreasing when \( \delta > 0 \). The second term is a parabola of vertical axis passing by \((0,0)\) and \((q,0)\) and taking negative values between them (which is the only region useful for our purpose). In the region where the function takes negative (resp. positive) values the equilibrium on \( x = 0 \) is transversally (i.e., with respect to small \( x \)) stable (resp. unstable). The stabilizing role of the parameter \( \delta \) is then apparent. Moreover, for \( \delta = 0 \), this equilibrium is transversally unstable when \( y_0 \) is nearby \( 0 \) or \( q \), whereas it may or not be stable in an intermediate region according to the values of the other parameters. When \( \delta > 0 \), the stability region is larger, but in any case it does not contain a neighbourhood of \( 0 \).

The previous considerations (as well as the analogous ones for \( y = 0 \)) are very useful to foresee or understand the location of the attractor of the three dimensional system (16). Roughly speaking, if the attractors in the invariant manifolds \( x = 0 \) and \( y = 0 \) are transversally unstable, there will be a global attractor involving the three species, whereas if the attractor on \( x = 0 \) (or \( y = 0 \)) is transversally stable, it will also be a three-dimensional attractor and the species \( x \) (or \( y \)) will disappear as \( t \nearrow +\infty \). Nevertheless, the previous considerations are only concerned with equilibria, not with periodic cycles or other. This is a serious drawback (which also applies to previous works on the problem, see for instance [1] section 5.10 and the references therein). An analogous study for periodic cycles is only possible by numerical computations on examples, which will be displayed in the next section.

6. Dependence on the vulnerabilities and a new paradox. We performed three computations (plots are displayed in figures 6, 7, 8, as well as a joint view of the three attractors in figure 9) of solutions of system (16) with all parameters equal for \( x \) and \( y \), unless the vulnerabilities. That of \( x \) was \( u = 1.4 \) and that of \( y \) was taken \( v = 1.2 \), \( v = 0.7 \) and \( v = 0.2 \) in the three computations. The other parameters were \( a = b = 1 \), \( c = 0.75 \), \( \delta = 0.2 \), \( p = q = 4 \).

In the first computation, the \( y \) are slightly less vulnerable than the \( x \) (\( u = 1.4 \) and \( v = 1.2 \)). It then appears a “three-dimensional attractor”, i.e., with non-vanishing \( x \), \( y \) and \( z \), in fact a periodic cycle (figure 6, as well as the three-dimensional view in figure 9). Obviously, the attractor is not symmetric in \( x \) and \( y \), it exhibits larger populations of \( y \) than of \( x \) (as the \( y \) are less vulnerable, so less consumed). It should be noted that this pattern is concerned with cycles, not equilibria, and it is out of the scope of the stability considerations at the end of section 5.

In the second computation, the \( y \) are frankly less vulnerable than the \( x \) (\( u = 1.4 \) and \( v = 0.7 \)). The advantage of the \( y \) is so important that the \( x \) disappear, i.e., the attractor is an equilibrium point on the plane \( x = 0 \) (figure 7, as well as the three-dimensional view in figure 9). This pattern agrees perfectly with the considerations on stability at the end of section 5; indeed, on the invariant manifold \( x = 0 \) the attractor is an equilibrium; moreover, it is in the intermediate region of values of \( y_0 \) where the equilibrium is transversally stable, i.e., it is a three-dimensional attractor.

This pattern is very interesting from the viewpoint of immediate versus mediate causality. We explained the process in terms of advantages of the \( x \) preys with respect to the \( y \) preys, but, from the viewpoint of the predator \( z \), it first eats the vulnerable preys \( x \), which disappear in the limit, and the attractor is only concerned
Figure 6. Plot of $x(t)$, $y(t)$, $z(t)$ for vulnerability $v = 1.2$.

Figure 7. Plot of $x(t)$, $y(t)$, $z(t)$ for vulnerability $v = 0.7$.

with the remaining (less vulnerable) preys $y$. In other words, during the transient, the predator enjoy good times, whereas the attractor (i.e. the long-term) is hard.

One may expect that the same pattern holds true for even smaller values of the vulnerability $v$ under the viability threshold of the predation of the $z$ on the $y$ (see Section 3), but this is not always true. Indeed, in our third computation (with $v = 0.2$ and always $u = 1.4$, see figure 8, as well as the three-dimensional view in figure 9) the attractor is again three-dimensional (i.e. with the three populations different from zero). It is again a periodic cycle, as in figure 6, but with a structure very different of it. Indeed, for $v = 1.2$ (figure 6) there was some kind of partnership between $x$ and $y$. Oppositely, for $v = 0.2$ (figure 8) the predators are basically fed with the vulnerable $x$, while the $y$, much less vulnerable, are some kind of secondary income. Indeed, it may be seen in figure 8 that the population $y(t)$ fluctuates not
Figure 8. Plot of $x(t)$, $y(t)$, $z(t)$ for vulnerability $v = 0.2$.

Figure 9. The attractors for vulnerability $v = 1.2$, $v = 0.7$ and $v = 0.2$.

far from the value $y = q = 4$ (the equilibrium of $y$ with its subsistences), whereas the $x(t)$ constitute the very food of the predator. There was some kind of recovering of $x$, which is only lost for intermediate values of $v$.

The recovering of $x$ for very small values of the vulnerability $v$ of the $y$ is striking, but it may nevertheless be explained as follows. As the vulnerability of the $y$ is lower than that of the $x$ (i.e., $v < u$), the $y$ certainly enjoy an advantage with respect to the $x$, but this advantage is not intrinsic, it is only effective in the presence of the predator $z$. More precisely, the advantage is most effective when the
predation process is significant, i.e., according to the considerations of Section 4, for intermediate values of the vulnerability. When the vulnerability of the $y$ becomes very small, the population of predators is also small, so that the predation process is not significant, and the advantage of the $y$ with respect to the $x$ disappears. This is a very intriguing phenomenon which certainly deserves of deeper study. We shall only point out here that it seems hold for large zones of the parameter space, even with differences between the other parameters of $x$ and $y$. As an example, it also holds for the values $a = 1$, $b = 1.2$, $c = 0.7$, $\delta = 0.6$, $p = 6$, $q = 4$, and the same values of the vulnerabilities, i.e. $u = 1.4$ and $v = 1.2$, $v = 0.7$ and $v = 0.2$ in three computations.

7. Complement. An example with oscillating vulnerability. According to the general features described in the previous section, one may wonder what happens when the vulnerability $v$ of the preys $y$ is a periodic function of time, with large period with respect to that of the intrinsic oscillations of the system. This is a very natural question, as vulnerability may oscillate according to seasons or any other environmental parameter. One may wonder if some kind of burst oscillations may appear. This is a complex question, as the various studies of the previous sections were by no means exhaustive; moreover, the swing between two configurations is not instantaneous, as it involves transients which are difficult to take into account.

We only give here an interesting numerical example. We consider again the system (16) with $a = b = 1$, $p = q = 4$, $\delta = 0$, $c = 0.75$, $u = 1.3$ and $v = 0.5(1 + \cos(0.03t))$. The plot of the predator population $z(t)$ appears in figure 10. There is a clear periodicity of large period and fast oscillations which are associated respectively with the imposed $v(t)$ and with the intrinsic oscillations, but the various patterns of the previous sections are not explicitly apparent inside each large period.

8. Conclusions. The causality scheme of a (essentially non symmetric) predator-prey system involves automatically advantages and disadvantages highly dependent on time. This is a widely known issue, often handled by popular wisdom; the fable
of the cricket (or the cicada) and the ant is a very pertinent study of the various ways of management of resources, usually associated with intentional forecast. But evolutionary biology is not concerned with forecasting, nor with teleological issues. Nevertheless, within the framework of the mathematical theory of dynamical systems, a thorough study of predator-prey systems, obviously independent of any kind of teleology, furnishes issues involving mediate and immediate causality (naturally associated with the attractor and the previous transient, respectively).

We discussed systems with a predator and one or two preys, and mainly the influence of the parameter accounting for the vulnerability of the preys. The main issues are:

- Generally speaking, small vulnerability leads to attractors which are equilibrium states, whereas large vulnerability lead to periodic cycles (stable periodic endogeneous states). (Section 4).

- When the vulnerability is small, an increase of it implies a (demographic) disadvantage for the preys, but, when it is large (involving periodic cycles) an increase turns out in an advantage because of the rarefaction of predators (this is associated with average populations on the periodic cycles). (Section 4).

- When two preys with different vulnerability are present, the most vulnerable may disappear (i.e. the attractor does not contain such prey). From the viewpoint of the predator, this is some kind of cricket-like behavior, as the transient and the attractor are respectively made of the most and less vulnerable preys. This phenomenon only occurs when the less vulnerable prey is nevertheless able to support the predator; otherwise, this one keeps eating anyway the other preys. In other words, according to the values of the two vulnerabilities, one of the two preys (the most vulnerable) may disappear, whereas the predator is always present (provided one of the vulnerabilities is larger than the threshold of viability). (Section 6).

The mechanism of such patterns (which in any case deserve a deeper study) are better described in terms of attractors and stability than in terms of advantages versus disadvantages (which are drastically dependent of the viewpoints of the three species).

REFERENCES

[1] F. Brauer and C. Castillo-Chavez, *Mathematical Models in Population Biology and Epidemiology*, Texts in Applied Mathematics, 40, Springer, New York, 2012.

[2] J-P. Françoise, Oscillations en biologie, *Analyse Qualitative et Modèles*, Mathématiques & Applications, 46, Springer-Verlag, Berlin, 2005.

[3] A. Klebanoff and A. Hastings, *Chaos in three-species food chains*, J. Math. Biol., 32 (1994), 427–451.

[4] P. Lherminier and E. Sanchez-Palencia, Remarks and examples on transient processes and attractors in biological evolution, *Proceedings of the 2014 Madrid Conference on Applied Mathematics*, Electron. J. Differ. Equ. Conf., 22, Texas State Univ., San Marcos, TX, 2015, 63–77.

[5] C. Lobry, *Modèles déterministes en Dynamique des Populations*, Ecole CIMPA Saint Louis du Sénégal, 2001.

[6] K. S. McCann, The diversity-stability debate, *Nature*, 405 (2000), 228–233.

[7] J. D. Murray, *Mathematical Biology. I: An Introduction*, Interdisciplinary Applied Mathematics, 17, Springer-Verlag, New York, 2002.

[8] K. Sigmund, *Kolmogorov and population dynamics*, in *Kolmogorov’s Heritage in Mathematics*, Springer, Berlin, 2007, 177–186.

[9] S. Smale, On the differential equations of species in competition, J. Math. Biol., 3 (1976), 5–7.
[10] A. Vidal, Periodic orbits of tritrophic slow-fast system and double homoclinic bifurcation, *Proceedings of the 6th AIMS International Conference*, 2007, 1021–1030.

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