

Prey gathering may act as a counterattack measure against predators

El agrupamiento de presas puede actuar como una medida de contraataque contra los depredadores.

Martina Cossa¹, Ester Cravero¹, Masaki Pugliese¹ and Ezio Venturino¹

¹ *Dipartimento di Matematica “Giuseppe Peano”, Università di Torino, via Carlo Alberto 10, 10123 Torino, Italy*

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Abstract—Two generalist predators not interfering with each other and hunting the same single prey that gathers in a herd are here considered. The system allows only two possible final outcomes, the prey-free state in which both predators thrive at their own carrying capacities, an equilibrium that is always present, and coexistence, which is not guaranteed to exist. When it arises, it does it in pair, of which one point is a saddle. As a result, the phase space is partitioned into two domains of attraction corresponding to these two equilibria. If the prey represents a pest, this result would provide a theoretical tool for its eradication, provided that it is coupled with some human external action, such as insecticide spraying, which however can be administered just in a mild way, sufficient to push the system trajectories into the prey-free point domain of attraction. If it is a species to be preserved instead, corresponding measures for enhancing its survival should be taken, such as increasing its reproductivity or lowering the predators’ pressure, so that the state of the system would fall into the attraction domain of the coexistence equilibrium.

Keywords—Mathematical Ecology, Mathematical Models, Population theory, Herding, Two-predators-one-prey

Resumen—Aquí se consideran dos depredadores generalistas que no interfieren entre sí y cazan la misma presa única que se reúne en una manada. El sistema permite solo dos posibles resultados finales, el estado libre de presas en el que ambos depredadores prosperan con sus propias capacidades de carga, un equilibrio que siempre está presente y la coexistencia, que no está garantizada. Cuando surge, lo hace en pareja, de las cuales un es un punto silla. Como resultado, el espacio de fases se divide en dos dominios de atracción correspondientes a estos dos equilibrios. Si la presa representa una plaga, este resultado proporcionaría una herramienta teórica para su erradicación, siempre que se acompañe de alguna acción externa humana, como la fumigación con insecticidas, que sin embargo puede administrarse de forma suave, suficiente para empujar las trayectorias del sistema en el dominio de atracción del punto libre de presas. Si en cambio se trata de una especie a preservar, se deben tomar las medidas correspondientes para mejorar su supervivencia, como aumentar su reproductividad o disminuir la presión de los depredadores, de modo que el estado del sistema caiga en el dominio de atracción del equilibrio de coexistencia.

Palabras clave— Modelos Matemáticos, Ecología Matemática, Teoría de las Poblaciones, Manadas, Dos-predadores-una-presa

INTRODUCTION

Several papers in the literature address the one-predator-several-prey situation, for instance in trophic chains as in (Baudrot et al., 2016a,b), where at times also the influence of contaminants and diseases are discussed, (Baudrot et al., 2018; Sieber et al., 2014).

Populations gathering in herds are well-known in nature. Herbivores usually have this habit and retain it also while

wandering in the prairies in search for better feeding and pastures. Modeling this specific feature has been addressed in a number of papers, starting from (Ajraldi et al., 2011). Herding has been a subject of recent researches also with situations envisaging a disease affecting some population in the system, (Belvisi and Venturino, 2013; Cagliero and Venturino, 2016; Kooi and Venturino, 2016). In other contexts several investigations have dealt with different and even generic response functions (González-Olivares et al., 2022; Vil-

ches et al., 2018) or have studied herding populations diffusion in space (Souana et al., 2020; Jiang and Tang, 2019). One of the results that most distinguishes these models from the classical ones is in (Melchionda et al., 2018), where tristability is discovered to take place in two competing populations, allowing the simultaneous thriving of both, in contrast to the classical result that for such a system competitive exclusion must occur.

In this paper we continue the study of prey gathered in herds. We keep on using a particular form of the response function, namely the square root function, but it should be remarked that the latter is just a particular instance, a more general formulation has been introduced in (Bulai and Venturino, 2017; Djilali, 2019) leading perhaps to a slightly more difficult analysis, without however any significant change in the results. Here, in particular we assume that, if their numbers are large enough, prey can respond to predators' attacks by some form of retaliation, thereby reducing the chance of being hunted. The main idea is exposed in (Acotto and Venturino, 2022) and has further been explored in the parallel paper (Bondi et al., 2022). In the present situation we introduce a different ecological situation than those considered in the previous two investigations.

The paper is organized as follows. We describe the model construction in the next section and turn to its analysis in the subsequent section. A final discussion concludes the paper.

MODEL SETUP

We consider a prey population N that gather together. Herding facilitates the possible predators' X capturing of the prey on the boundary of the herd, expressed mathematically by the function $h(N, X)$. This is simply modeled via a square root function, assimilating the herd shape to a circle, although more general exponents other than $1/2$ can be taken, as discussed in (Bulai and Venturino, 2017), to account for more complicated domains, without any substantial changes in the results. Thus h has the form

$$h(N, X) = a\sqrt{NX}.$$

Here, specifically, two predators P and Q are present in the environment, and hunt the prey. The two predators are assumed to have also other food sources, and thereby do not explicitly compete with each other, only "mildly" through sharing the common prey N . Following the ideas of (Acotto and Venturino, 2022), the predators' attacks are reduced if the prey population attains a sufficiently large size. Therefore to model the functional response, we need a decreasing function of N , that vanishes in the limit when N tends to infinity. Thus, the function $h(N, X)$ should be a kind of modified Holling type II (HTII) response function, and thus must be modified as follows

$$h(N, X) = a \frac{\sqrt{NX}}{1 + bN}. \tag{1}$$

These considerations lead to the system

$$\begin{aligned} \frac{dP}{dt} &= n_P P \left(1 - \frac{P}{H_P}\right) + \frac{e_P a_P \sqrt{NP}}{1 + b_P N}, \\ \frac{dQ}{dt} &= n_Q Q \left(1 - \frac{Q}{H_Q}\right) + \frac{e_Q a_Q \sqrt{NQ}}{1 + b_Q N}, \\ \frac{dN}{dt} &= n_N N \left(1 - \frac{N}{H_N}\right) - \frac{a_P \sqrt{NP}}{1 + b_P N} - \frac{a_Q \sqrt{NQ}}{1 + b_Q N}. \end{aligned} \tag{2}$$

The first two equations for the predators are similar, containing a logistic term expressing the availability of other resources, and the benefit from hunting the prey N , scaled via suitable conversions coefficients e_P and e_Q , where the functional response of type (1) has been employed. The third equation for the prey N also has a logistic growth rate, but the additional terms express the harm suffered by the predators' attacks. All the parameters are assumed to be nonnegative, in particular the reproduction rates n_P and n_Q are here strictly positive:

$$n_P > 0, \quad n_Q > 0. \tag{3}$$

Table 1 lists all the model parameters and their interpretation.

Parameter	Interpretation
H_P	predator P carrying capacity
H_Q	predator Q carrying capacity
H_N	prey N carrying capacity
n_P	predator P reproduction rate
n_Q	predator Q reproduction rate
n_N	prey N reproduction rate
e_P	predator P conversion coefficient
e_Q	predator Q conversion coefficient
a_P	predator P hunting rate
a_Q	predator Q hunting rate
b_P	predator P handling time
b_Q	predator Q handling time

TABLE 1: PARAMETER INTERPRETATION FOR MODEL (2).

THE SYSTEM BEHAVIOR

We study here the dynamics of (2), focusing on its possible equilibria. The analysis will assess their feasibility and local stability.

Equilibria feasibility

The equilibrium equations obtained from (2) are highly nonlinear, but in some simple instances, analytic expressions for the equilibrium population values can be obtained. There are eight possible combinations, if we concentrate on the two alternatives that a population may or may not be present in the environment. All of them are at least conditionally admissible, as we will see below. This essentially follows from the assumption that the predators are generalist, which prevents the rejection of the points containing only such populations in the absence of their prey N based on the fact that for specialist predators this is their only food source.

Equilibria with just one population

Easily, the points $E_0 = (0,0,0)$, $E_N = (0,0,H_N)$, $E_Q = (0,H_Q,0)$ and $E_P = (H_P,0,0)$ are seen to be unconditionally feasible.

Equilibria with just two populations

The same results as for the single population points hold also for the prey-free point $E_{PQ} = (H_P, H_Q, 0)$.

The other equilibria with two populations are more involved. But the symmetrical nature of the system (2) in terms of the two predators, allows us to investigate only one of them, as for the other one the results will follow by a simple change in the subscript.

Prey-one-predator equilibrium $E_{QN} = (0, \tilde{Q}^*, \tilde{N}^*)$

We thus investigate the point with $P = 0$, $Q \neq 0$, $N \neq 0$. From the last two equilibrium equations of (2), we obtain the nonlinear system

$$\begin{aligned}\Phi(N) &= \Phi_Q(N) = \frac{H_Q}{n_Q} \left(n_Q + \frac{e_Q a_Q \sqrt{N}}{1 + b_Q N} \right), \\ \Psi(N) &= \Psi_Q(N) = \frac{n_N}{a_Q} \sqrt{N} \left(1 - \frac{N}{H_N} \right) (1 + b_Q N).\end{aligned}\quad (4)$$

The possible solution of this system will be investigated geometrically, as the intersections of the two curves $\Phi(N)$ and $\Psi(N)$. The height of these points therefore provide the predators equilibrium value \tilde{Q}^* , while the abscissae those of \tilde{N}^* , so that the point $E_{QN} = (0, \tilde{Q}^*, \tilde{N}^*)$ is known.

The function $\Phi(N)$ is defined over the whole positive line, with height at the origin given by H_N and a horizontal asymptote at the same level, in view of the following result

$$\lim_{N \rightarrow \infty} \Phi(N) = H_Q^+,$$

the asymptote being approached from above. Evaluating its derivative, we find

$$\Phi'(N) = \frac{H_Q e_Q a_Q (1 - b_Q N)}{2n_Q \sqrt{N} (1 + b_Q N)^2}$$

where the denominator is always positive. To assess the sign of $\Phi'(N)$ we just need to study the one of the numerator, which is positive for $N < \frac{1}{b_Q}$. Thus for $0 < N < \frac{1}{b_Q}$ the function $\Phi(N)$ is increasing, and conversely decreasing in $N > \frac{1}{b_Q}$. The maximum is thus attained at the point

$$M_\Phi = \left[\frac{1}{b_Q}, \Phi \left(\frac{1}{b_Q} \right) \right].$$

In view of the above findings, it is apparent that near the origin $\Phi(N)$ is concave, because

$$\lim_{N \rightarrow 0^+} \Phi'(N) = +\infty,$$

and it becomes convex for large values of N , indicating the presence of an inflection point. To assess it better, we differentiate once more,

$$\Phi''(N) = \frac{e_Q a_Q H_Q (3N^2 b_Q^2 - 6N b_Q - 1)}{4n_Q N \sqrt{N} (1 + b_Q N)^3}.$$

Again, the denominator does not influence the sign of the second derivative. In the numerator the term $3N^2 b_Q^2 - 6N b_Q - 1$ is positive whenever $N < N_{\Phi''}^-$ and $N > N_{\Phi''}^+$, where $N_{\Phi''}^\pm$ are its zeros,

$$N_{\Phi''}^\pm = \frac{1}{3b_Q^2} \left[3b_Q \pm \sqrt{9b_Q^2 + 3b_Q^2} \right] = \frac{1}{3b_Q^2} \left[3b_Q \pm 2b_Q \sqrt{3} \right]$$

that always exist as the discriminant of the corresponding quadratic equation is always positive. Specifically,

$$N_{\Phi''}^- = \frac{1}{3b_Q} \left[3 - 2\sqrt{3} \right] < 0, \quad N_{\Phi''}^+ = \frac{1}{3b_Q} \left[3 + 2\sqrt{3} \right] > 0.$$

In conclusion, $\Phi(N)$ is convex for $0 < N < N_{\Phi''}^+$ and it is concave for $N > N_{\Phi''}^+$.

Qualitatively, the behavior of $\Phi(N)$ is shown in Figure 1.

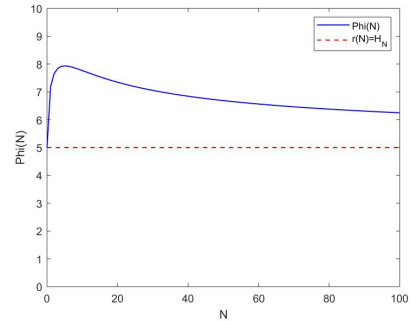


Figure 1: The function $\Phi(N)$ for the parameter choice $n_Q = 0,4$, $H_Q = 5$, $e_Q = 0,3$, $a_Q = 0,7$, $b_Q = 0,2$.

We now study the function $\Psi(N)$. It is defined for all $N \geq 0$ and

$$\lim_{N \rightarrow \infty} \Psi(N) = -\infty.$$

Its zeros are located at the origin and at $\psi_1 = H_N$, while the other vanishing point $\psi_2 = -b_Q^{-1} < 0$ lies outside the relevant domain of interest. On calculating its derivative, the denominator is found to be always positive,

$$\Psi'(N) = \frac{-n_N [5b_Q N^2 - 3N(b_Q H_N - 1) - H_N]}{2a_Q H_N \sqrt{N}},$$

and the sign of $\Psi'(N)$ depends just on the one of the numerator, which is the quadratic function

$$q(N) = -5b_Q N^2 + 3N(b_Q H_N - 1) + H_N.$$

Specifically $\Psi'(N) > 0$ within the interval of the roots $N_{\Psi'}^\pm$, with

$$\begin{aligned}N_{\Psi'}^- &= -\frac{1}{10b_Q} \left[3(b_Q H_N - 1) - \sqrt{9(1 - b_Q H_N)^2 + 20b_Q H_N} \right], \\ N_{\Psi'}^+ &= -\frac{1}{10b_Q} \left[3(b_Q H_N - 1) + \sqrt{9(1 - b_Q H_N)^2 + 20b_Q H_N} \right].\end{aligned}$$

Note that they are always real, because $q(0) = H_N > 0$ and $q(N)$ is a concave parabola. Also, we have $N_{\Psi'}^+ < 0$ and $N_{\Psi'}^- > 0$, in both cases $b_Q H_N > 1$ and $b_Q H_N < 1$. Thus $\Psi(N)$ is increasing for $0 < N < N_{\Psi'}^-$ and decreasing in $[N_{\Psi'}^-, \infty)$, so

that its maximum is located at the point $(N_{\Psi'}^+, \Psi(N_{\Psi'}^+))$. We study now the second derivative

$$\Psi''(N) = \frac{-n_N[15b_QN^2 - 3N(b_QH_N - 1) + H_N]}{4a_QH_NN\sqrt{N}},$$

where the denominator is once more always positive in the domain of interest, $N > 0$. To assess convexity, we investigate the sign of the numerator, which is positive in case

$$p(N) = 15b_QN^2 - 3N(b_QH_N - 1) + H_N \leq 0.$$

The roots of $p(N) = 0$ are

$$N_{\Psi''}^{\pm} = \frac{1}{30b_Q} [3(b_QH_N - 1) \pm \sqrt{\Delta}], \quad (5)$$

where Δ is regarded as a function of b_QH_N :

$$\Delta = 9(b_QH_N - 1)^2 - 60b_QH_N = 9(b_QH_N)^2 - 78b_QH_N + 9.$$

In turn Δ is a quadratic function in $\delta = b_QH_N$, with roots

$$\delta_{\pm} = \frac{1}{9} [39 \pm \sqrt{1521 - 81}] = \frac{1}{9} [39 \pm \sqrt{1440}] \approx \frac{1}{9} [39 \pm 37,95]$$

that are both positive. Thus $\Delta > 0$ in both the following alternative cases:

$$0 < b_QH_N < \delta_- = \delta_1 \approx 0,12, \quad b_QH_N > \delta_+ = \delta_2 \approx 8,55.$$

With these restrictions this guarantees the existence of real roots for the numerator of the second derivative of Ψ , namely $N_{\Psi''}^{\pm}$.

There are two cases:

- If $\Delta < 0$, $N_{\Psi''}^-$ and $N_{\Psi''}^+$ are both complex, the quadratic $p(N)$ is always positive and thus $\Psi''(N) < 0$ entailing that the function $\Psi(N)$ is always concave for $N > 0$.
- Alternatively for $\Delta > 0$, we may have either $0 < b_QH_N < \delta_1 < 1$ or $b_QH_N > \delta_2 > 8$.

Note that for $b_QH_N < 1$, from (5) we find $N_{\Psi''}^{\pm} < 0$, because $\Delta < 3(b_QH_N - 1)$. In such case $\Psi''(N) < 0$ outside the interval $[N_{\Psi''}^-, N_{\Psi''}^+]$, and in particular for all $N > 0$. Hence in the domain of interest, Ψ is concave.

If instead $b_QH_N > 1$, again using (5) we have $N_{\Psi''}^{\pm} > 0$, once more because $\Delta < 3(b_QH_N - 1)$. But this and $\Delta > 0$ imply that $b_QH_N > \delta_2 > 8$, so that either

$$0 < N_{\Psi''}^- < \delta_1 < 1, \quad N_{\Psi''}^+ > \delta_2 > 8,$$

or, alternatively

$$N_{\Psi''}^{\pm} > \delta_2 > 8.$$

In both cases, it turns out that $\Psi''(N) > 0$ for $N_{\Psi''}^- < N < N_{\Psi''}^+$, which implies that $\Psi(N)$ is convex in the same interval $[N_{\Psi''}^-, N_{\Psi''}^+]$, and concave for $0 < N < N_{\Psi''}^-$ as well as for $N > N_{\Psi''}^+$.

These possible inflection points lie in the first quadrant only if the condition $\Psi(N_{\Psi''}^{\pm}) > 0$ is satisfied.

The equilibrium E_{QN} is therefore a possible intersection of $\Phi(N)$ and $\Psi(N)$ in the first quadrant. Now, in view of the

above analysis, this is not always guaranteed, as it is clear from Figure 2. It is also apparent that the two intersections, giving a pair of equilibria, occur via a saddle-node bifurcation.

A sufficient condition for the existence of such points is obtained when the maximum value of $\Psi(N)$ exceeds the value of $\Phi(N)$ for the corresponding abscissa. Obviously, the latter is located at the zero $N_{\Psi'}^+$ of $\Psi'(N)$ and thus the sufficient condition reads

$$\Phi(N_{\Psi'}^+) \geq \Psi(N_{\Psi'}^+). \quad (6)$$

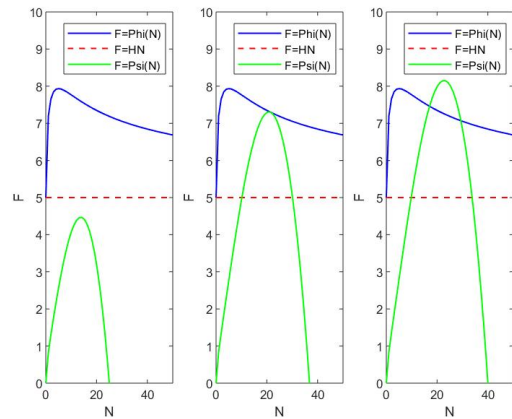


Figure 2: Graph of the functions $\Psi(N)$ and $\Phi(N)$ with the parameters $a_Q = 0,7$, $b_Q = 0,2$, $e_Q = 0,3$, $n_N = 0,5$, $n_Q = 0,4$, $H_Q = 5$. Left to right, $H_N = 25$, $H_N = 38,6$ and $H_N = 40$.

Equilibrium with the other predator absent $(\hat{P}^*, 0, \hat{N}^*)$

As stated above, this case can be investigated in the same way as for $E_{QN} = (0, \tilde{Q}^*, \tilde{N}^*)$, by suitably changing the notation. The sufficient condition (6) would be replaced by an analogous statement, where $\Phi(N)$ and $\Psi(N)$ would be meant to be the functions $\Phi_P(N)$ and $\Psi_P(N)$ with an obvious change of notation in (4).

Coexistence equilibrium

We study this equilibrium $E^* = E_{PQN} = (P^*, Q^*, N^*)$ by solving two of the equilibrium equations and substituting into the remaining one. From the first two equilibrium equations we find

$$P = \frac{H_P}{n_P} \left(n_P + \frac{e_P a_P \sqrt{N}}{1 + b_P N} \right)$$

and

$$Q = \frac{H_Q}{n_Q} \left(n_Q + \frac{e_Q a_Q \sqrt{N}}{1 + b_Q N} \right).$$

Substitution into the equilibrium equation for N we obtain the equation

$$\beta(N) = 0,$$

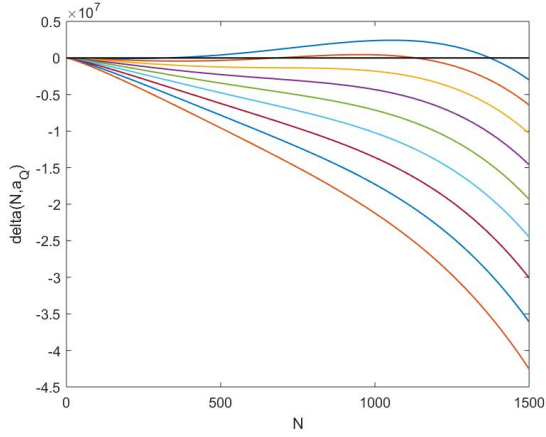


Figure 3: The figure shows the behavior of $\beta(N)$ as a function of $a_Q \in [0,1,0,9]$, where all other parameters are given in (8).

where

$$\beta(N) = n_N N \left(1 - \frac{N}{H_N} \right) - \frac{a_P \sqrt{N} H_P [n_P (1 + b_P N) + e_P a_P \sqrt{N}]}{n_P (1 + b_P N)^2} - \frac{a_Q \sqrt{N} H_Q [n_Q (1 + b_Q N) + e_Q a_Q \sqrt{N}]}{n_Q (1 + b_Q N)^2}. \quad (7)$$

The function $\beta(N)$ is explored numerically for the assessment of its possible zeros. For this task we use the following set of parameters:

$$\begin{aligned} n_N = 0,3, \quad n_P = 0,4, \quad n_Q = 0,3, \quad H_P = 150, \quad (8) \\ H_Q = 1200, \quad H_N = 1500, \quad e_P = 0,8, \quad e_Q = 0,9, \\ a_P = 0,8, \quad a_Q = 0,2, \quad b_P = 0,4, \quad b_Q = 0,1. \end{aligned}$$

Figure 3 contains the plots of $\beta(N)$ for nine choices of the parameter a_Q , the predator Q hunting rate, in the interval $[0,1,0,9]$, while all the remaining ones are taken from (8). Similarly in Figure 4 the varying parameter, in the same interval, is n_N , the prey N birth rate. Finally in Figure 5 we let n_Q , the predator Q birth rate, change. These three parameters have been selected because they appear to be the most important ones to influence the behavior of $\beta(N)$. Further, in all cases, it is seen that the number of the nontrivial roots changes, it may be zero, or up to two. Therefore the coexistence equilibrium is not guaranteed always to exist. Also, whenever it arises, it does it in pairs, through a saddle-node bifurcation.

Equilibria stability

To assess local stability, we need the Jacobian of (2):

$$J = \begin{bmatrix} J_{1,1} & 0 & J_{1,3} \\ 0 & J_{2,2} & J_{2,3} \\ J_{3,1} & J_{3,2} & J_{3,3} \end{bmatrix},$$

with

$$\begin{aligned} J_{1,1} &= n_P \left(1 - \frac{2P}{H_P} \right) + \frac{e_P a_P \sqrt{N}}{1 + b_P N} \\ J_{1,3} &= \frac{e_P a_P P}{2\sqrt{N}(1 + b_P N)^2} \end{aligned}$$

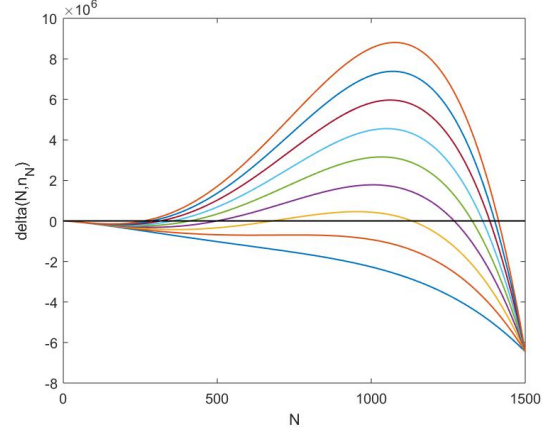


Figure 4: The figure shows the behavior of $\beta(N)$ as a function of $n_N \in [0,1,0,9]$, where all other parameters are given in (8).

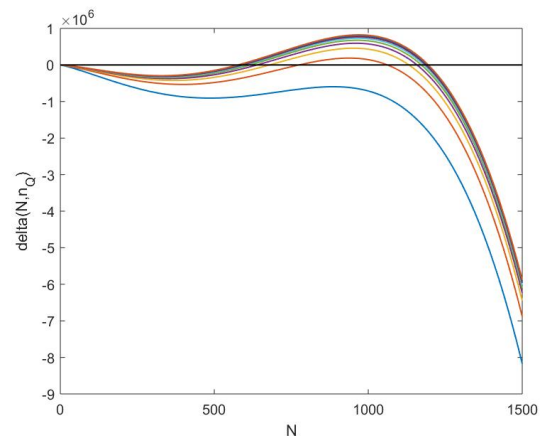


Figure 5: The figure shows the behavior of $\beta(N)$ as a function of $n_Q \in [0,1,0,9]$, where all other parameters are given in (8).

$$J_{2,2} = n_Q \left(1 - \frac{2Q}{H_Q} \right) + \frac{e_Q a_Q \sqrt{N}}{1 + b_Q N}$$

$$J_{2,3} = \frac{e_Q a_Q Q}{2\sqrt{N}(1 + b_Q N)^2}$$

$$J_{3,1} = -\frac{a_P \sqrt{N}}{1 + b_P N}$$

$$J_{3,2} = -\frac{a_Q \sqrt{N}}{1 + b_Q N}$$

$$J_{3,3} = n_N \left(1 - \frac{2N}{H_N} \right) - \frac{a_P P}{2\sqrt{N}(1 + b_P N)^2} - \frac{a_Q Q}{2\sqrt{N}(1 + b_Q N)^2}$$

Because the equilibria with $N = 0$ will have a singularity in the Jacobian, we will analyse them separately.

Equilibria with $N \neq 0$

At the point $E_N = (0, 0, H_N)$ the Jacobian becomes a lower triangular matrix, with eigenvalues along the diagonal:

$$n_P + \frac{e_P a_P \sqrt{H_N}}{1 + b_P H_N} > 0, \quad n_Q + \frac{e_Q a_Q \sqrt{H_N}}{1 + b_Q H_N} > 0, \quad -n_N < 0$$

and unconditional instability follows from the positivity of the first two.

For $E_{PN} = (\hat{P}^*, 0, \hat{N}^*)$ one eigenvalue is immediately known, as the Jacobian factorizes:

$$J_{2,2} = n_Q + \frac{e_Q a_Q \sqrt{\hat{N}^*}}{1 + b_Q \hat{N}^*} > 0$$

and this is enough to ensure once again unconditional instability.

A similar result holds for $E_{QN} = (0, \tilde{Q}^*, \tilde{N}^*)$, for which

$$J_{1,1} = n_P + \frac{e_P a_P \sqrt{\tilde{N}^*}}{1 + b_P \tilde{N}^*} > 0$$

and also this point is always unstable.

For coexistence $E^* = E_{PQN} = (P^*, Q^*, N^*)$, note the simplifications:

$$J_{1,1}(E^*) = -n_P \frac{P^*}{H_P}, \quad J_{2,2}(E^*) = -n_Q \frac{Q^*}{H_Q},$$

$$J_{3,3}(E^*) = \frac{a_P P^*(1 + 2b_P N^*)}{2\sqrt{N^*}(1 + b_P N^*)^2} + \frac{a_Q Q^*(1 + 2b_Q N^*)}{2\sqrt{N^*}(1 + b_Q N^*)^2} - n_N \frac{N^*}{H_N}.$$

To assess stability we apply the Routh-Hurwitz conditions. The one on the trace gives

$$\begin{aligned} & \frac{a_P P^*(1 + 2b_P N^*)}{2\sqrt{N^*}(1 + b_P N^*)^2} + \frac{a_Q Q^*(1 + 2b_Q N^*)}{2\sqrt{N^*}(1 + b_Q N^*)^2} \\ & < n_P \frac{P^*}{H_P} + n_Q \frac{Q^*}{H_Q} + n_N \frac{N^*}{H_N}. \end{aligned} \quad (9)$$

The sum of the principal minors of order two is

$$\begin{aligned} M_2^* &= n_P \frac{P^*}{H_P} n_Q \frac{Q^*}{H_Q} - n_P \frac{P^*}{H_P} J_{3,3}(E^*) \\ &+ \frac{a_P \sqrt{N^*}}{1 + b_P N^*} \frac{e_P a_P P^*}{2\sqrt{N^*}(1 + b_P N^*)^2} - n_Q \frac{Q^*}{H_Q} J_{3,3}(E^*) \\ &+ \frac{a_Q \sqrt{N^*}}{1 + b_Q N^*} \frac{e_Q a_Q Q^*}{2\sqrt{N^*}(1 + b_Q N^*)^2} \end{aligned} \quad (10)$$

We now evaluate the determinant:

$$\begin{aligned} \det(J(E^*)) &= n_P \frac{P^*}{H_P} n_Q \frac{Q^*}{H_Q} J_{3,3}(E^*) \\ &- \frac{n_Q e_P a_P^2 P^* Q^*}{2H_Q(1 + b_P N^*)^3} - \frac{n_P e_Q a_Q^2 P^* Q^*}{2H_P(1 + b_Q N^*)^3} \end{aligned} \quad (11)$$

to establish its positivity, giving the condition

$$\begin{aligned} \frac{n_P n_Q P^* Q^*}{H_P H_Q} J_{3,3}(E^*) &> \frac{n_Q e_P a_P^2 P^* Q^*}{2H_Q(1 + b_P N^*)^3} \\ &+ \frac{n_P e_Q a_Q^2 P^* Q^*}{2H_P(1 + b_Q N^*)^3} \end{aligned} \quad (12)$$

The last requirement for stability, which we leave in a synthetic form, reads

$$\text{tr}(J(E^*)) M_2^* < \det(J(E^*)). \quad (13)$$

These conditions define a set in the parameter space that is nonempty. This statement arises from the numerical simulations, that indeed indicate that this point $E^* = E_{PQN}$ can be stably achieved, showing also that the feasibility conditions discussed formerly are satisfied for some parameter choices. Figures 6-9 show the various possibilities, in terms of the possible locations of the roots of the function $\beta(N)$. In particular note that whenever two such roots exist, one of them (the smaller one) leads to an unstable coexistence equilibrium, as it should be expected as the latter arises through a saddle-node bifurcation as remarked earlier. For the same reason we observe that in the top frame of Figure 9, when both roots coalesce, the equilibrium that is generated is also unstable.

Equilibria with $N = 0$

Observing the dominant behavior of the system near E_0 , we have

$$\begin{aligned} \frac{dP}{dt} &= n_P P \left(1 - \frac{P}{H_P} \right) + \frac{e_P a_P \sqrt{N} P}{1 + b_P N} \\ &\approx P [n_P + e_P a_P \sqrt{N}] \approx n_P P > 0, \\ \frac{dQ}{dt} &= n_Q Q \left(1 - \frac{Q}{H_Q} \right) + \frac{e_Q a_Q \sqrt{N} Q}{1 + b_Q N}, \\ &\approx Q [n_Q + e_Q a_Q \sqrt{N}] \approx n_Q Q > 0, \\ \frac{dN}{dt} &= n_N N \left(1 - \frac{N}{H_N} \right) - \frac{a_P \sqrt{N} P}{1 + b_P N} - \frac{a_Q \sqrt{N} Q}{1 + b_Q N} \\ &\approx \sqrt{N} [n_N \sqrt{N} - (a_P P + a_Q Q)], \end{aligned}$$

and the consequence is unconditional instability due to the signs of the right hand sides of the first two equations.

For $E_P = (H_P, 0, 0)$, we find

$$\begin{aligned} \frac{dN}{dt} &= n_N N \left(1 - \frac{N}{H_N} \right) - \frac{a_P \sqrt{N} P}{1 + b_P N} - \frac{a_Q \sqrt{N} Q}{1 + b_Q N} \approx \sqrt{N} [n_N \sqrt{N} \\ &- (a_P(P - H_P) + a_P H_P + a_Q(Q - H_Q) + a_Q H_Q)] \\ &\approx -\sqrt{N} (a_P H_P + a_Q H_Q) < 0, \end{aligned}$$

so that along the N -axis the behavior is stable.

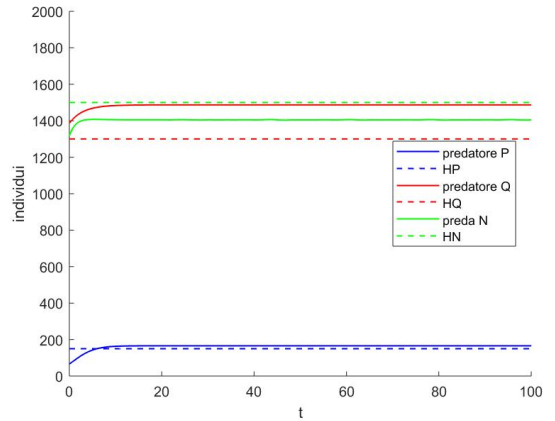
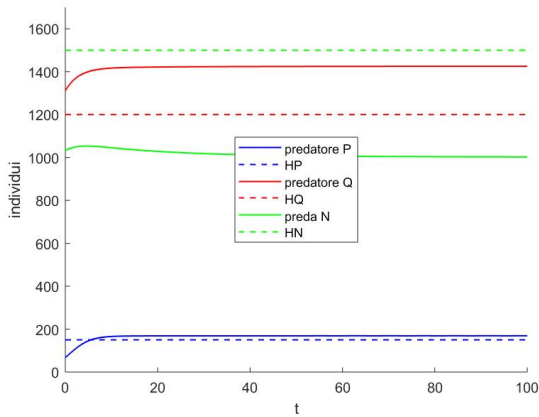
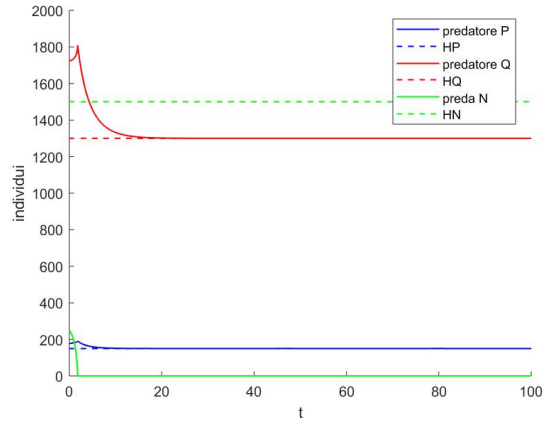
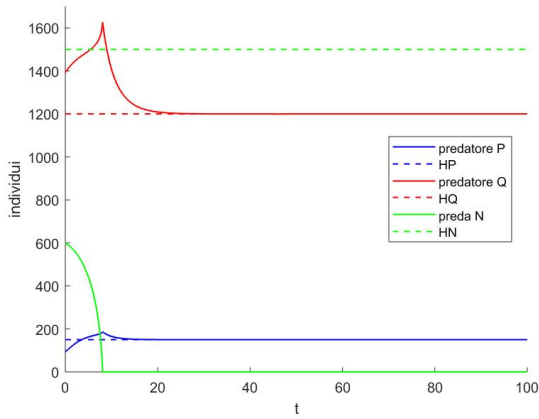


Figure 6: Coexistence obtained with the following parameter values: $n_N = 0,3$, $n_P = 0,4$, $n_Q = 0,3$, $H_P = 150$, $H_Q = 1200$, $H_N = 1500$, $e_P = 0,8$, $e_Q = 0,9$, $a_P = 0,8$, $a_Q = 0,2$, $b_P = 0,4$, $b_Q = 0,1$. The top frame corresponds to the initial condition near the zero $N_{1,\beta} = 678,6517$ of the function $\beta(N)$, which is seen to give an unstable equilibrium; the bottom one to the initial condition taken near the zero $N_{2,\beta} = 1132,4$, corresponding to a stable coexistence equilibrium.

Figure 7: Coexistence obtained with the following parameter values: $n_N = 0,9$, $n_P = 0,4$, $n_Q = 0,3$, $H_P = 150$, $H_Q = 1300$, $H_N = 1500$, $e_P = 0,8$, $e_Q = 0,9$, $a_P = 0,8$, $a_Q = 0,9$, $b_P = 0,4$, $b_Q = 0,5$. The top frame corresponds to the initial condition near the zero $N_{1,\beta} = 258,6319$ of the function $\beta(N)$, which is seen to give an unstable equilibrium; the bottom one to the initial condition taken near the zero $N_{2,\beta} = 1416,4$, corresponding to a stable coexistence equilibrium.

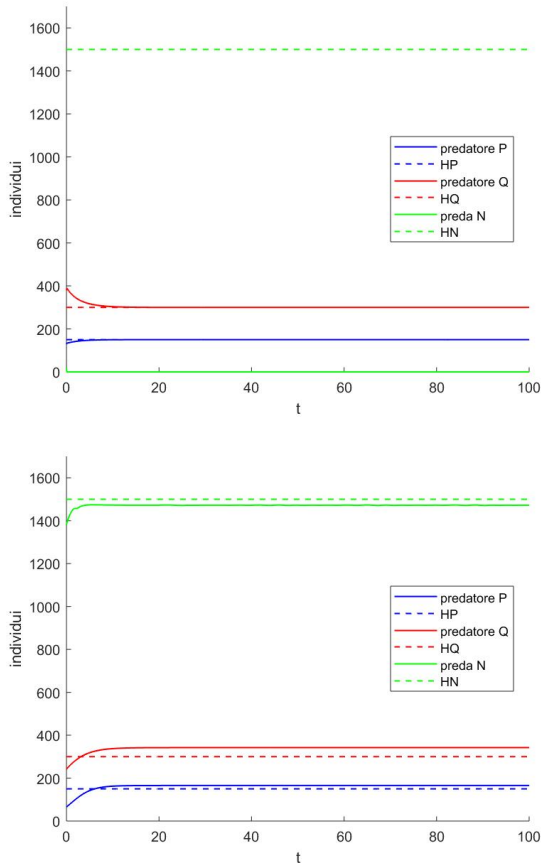


Figure 8: Coexistence obtained with the following parameter values: $n_N = 0,9$, $n_P = 0,4$, $n_Q = 0,3$, $H_P = 150$, $H_Q = 300$, $H_N = 1500$, $e_P = 0,8$, $e_Q = 0,9$, $a_P = 0,8$, $a_Q = 0,9$, $b_P = 0,4$, $b_Q = 0,5$. The top frame corresponds to the initial condition near the zero $N_{1,\beta} = 97,9228$ of the function $\beta(N)$, which is seen to give an unstable equilibrium; the bottom one to the initial condition taken near the zero $N_{2,\beta} = 1482,0$, corresponding to a stable coexistence equilibrium.

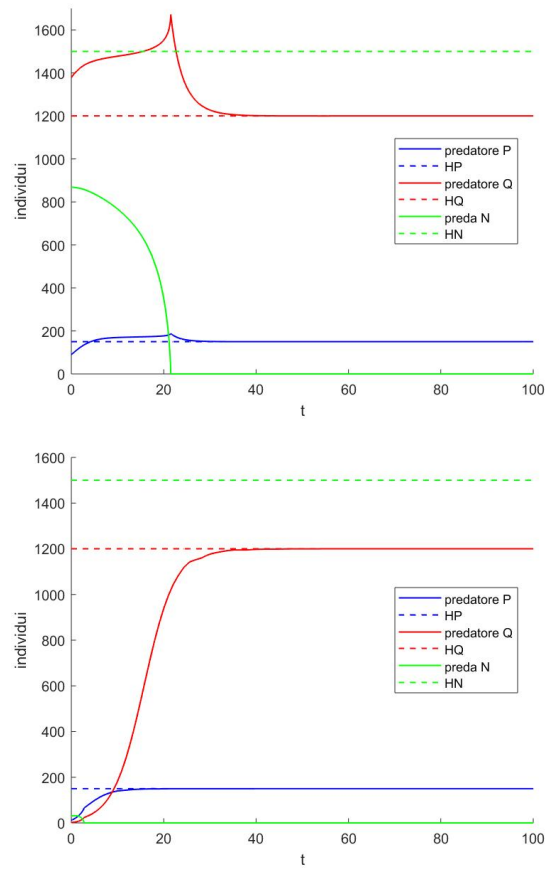


Figure 9: Top frame. Coexistence obtained with the following parameter values: $n_N = 0,3$, $n_P = 0,4$, $n_Q = 0,3$, $H_P = 150$, $H_Q = 1200$, $H_N = 1500$, $e_P = 0,8$, $e_Q = 0,9$, $a_P = 0,8$, $a_Q = 0,445$, $b_P = 0,4$, $b_Q = 0,2$. In this case the function $\beta(N)$ has just one zero, $N_{1,\beta} = 948,2506$, for which coexistence is unstable, the prey drifting to negative values and vanishing in a finite time. Bottom frame. Coexistence obtained with the following parameter values: $n_N = 0,3$, $n_P = 0,4$, $n_Q = 0,3$, $H_P = 150$, $H_Q = 1200$, $H_N = 1500$, $e_P = 0,8$, $e_Q = 0,9$, $a_P = 0,8$, $a_Q = 0,8$, $b_P = 0,4$, $b_Q = 0,2$. In this case the function $\beta(N)$ does not possess positive zeros. Again, the corresponding coexistence equilibrium is not attained.

TABLE 2: FEASIBILITY OF ALL THE EQUILIBRIA OF THE SYSTEM (2)

Equilibrium	Feasibility conditions
$E_0 = (0, 0, 0)$	–
$E_N = (0, 0, H_N)$	–
$E_Q = (0, H_Q, 0)$	–
$E_P = (H_P, 0, 0)$	–
$E_{QN} = (0, Q^*, N^*)$	$\Phi_Q(N) \cap \Psi_Q(N)$ sufficient: $\Phi_Q(N_{\Psi^+}^+) \geq \Psi_Q(N_{\Psi^+}^+)$
$E_{PN} = (P^*, 0, N^*)$	$\Phi_P(N) \cap \Psi_P(N)$ sufficient: $\Phi_P(N_{\Psi^+}^+) \geq \Psi_P(N_{\Psi^+}^+)$
$E_{PQ} = (H_P, H_Q, 0)$	–
$E^* = E_{PQN} = (P^*, Q^*, N^*)$	Arising through saddle-node bifurcation

The remaining minor of the Jacobian becomes a diagonal matrix, as no mutual interactions of the two predators are present:

$$\hat{J} = \begin{bmatrix} n_P \left(1 - \frac{2P}{H_P}\right) & 0 \\ 0 & n_Q \left(1 - \frac{2Q}{H_Q}\right) \end{bmatrix}$$

giving the eigenvalues $-n_P$ and $n_Q > 0$, thereby implying unconditional instability.

For the point $E_Q = (0, H_Q, 0)$ a similar result would hold as for E_P along the N axis. Again the submatrix of the Jacobian is diagonal, with eigenvalues $n_P > 0$ and $-n_Q$, showing once again instability.

However at the point $E_{PQ} = (H_P, H_Q, 0)$, these eigenvalues are both negative, $-n_P$ and $-n_Q$, implying for this equilibrium unconditional stability. The fact that these eigenvalues are real prevents any possible occurrence of a Hopf bifurcation at this point.

DISCUSSION

In the Tables 2 and 3 we summarize all the equilibria behavior, giving their feasibility and stability conditions.

Ultimately, only two outcomes are possible. Either the prey disappear, and the two predators thrive at their carrying capacities, E_{PQ} , or the three populations coexist, E_{PQN} . In the former case the predators natural population levels H_P and H_Q are undisturbed since they are assumed not to interfere with each other. Furthermore, in this situation no persistent oscillations can arise. Thus the predators are always found at a stable level, as this point is unconditionally feasible and stable. Note also that this result implies that in the system the predator populations are always present, independently of what happens for the other possible equilibrium.

Coexistence is instead not guaranteed to arise. If it does, its onset occurs through a saddle-node bifurcation, which implies the simultaneous appearance of two such points, of which the one with the lower level of prey N is unstable. This saddle point partitions the phase space through a separating surface, so that two domains of attractions exist, one being the one of the prey-free equilibrium E_{PQ} and the other one of the coexistence point $E^* = E_{PQN}$. Thus the ultimate behavior of the system trajectories would in such case depend only on

the present state of the system, i.e. the location of the initial condition.

The result that equilibrium E_{PQ} is unconditionally stable, coupled with the fact that two coexistence equilibria may arise in pairs, of which one unstable and one stable, as discussed above, indicates that in suitable circumstance bistability can be obtained.

Indeed, Figures 6-9 show graphically this behavior. In each case, for the same set of parameter values, the system trajectories tend to different equilibria, the prey-free point E_{PQ} in the top frame and coexistence E_{PQN} in the bottom one, just by changing the initial conditions, i.e. depending on the domain of attraction of which point the current state of the system is located. This result can suitably be exploited, so that at last bistability may result to be a very much important tool for addressing two relevant ecological problems, namely species eradication and preservation.

In case the prey is a nuisance, bistability could be exploited for its eradication, simply by trying to push the state of the system in the domain of attraction of the prey-free point E_{PQ} . To achieve this task, two important remarks should be made. First of all, such a “push” could be obtained by external, human driven means, such as insecticide spraying. Secondly, the external measure should be exerted in an amount small enough just to cross the separating surface, thereby also saving on costs.

If N is a species to be preserved instead, corresponding measures for its survival should be taken, so that the state of the system would be moved into the attraction domain of the coexistence equilibrium. Enhancing the chances of the species N to be preserved to survive could be achieved once more by external means, such as fostering its reproductivity or increasing its carrying capacity, or measures apt to reduce the predators hunting pressure. In the last case, for instance, a “measured” culling could be decided to be undertaken, sufficient enough to move the system trajectories into the coexistence equilibrium domain of attraction, thereby allowing the survival of the endangered species together with the two generalist predators.

Note that in the above discussion, the role of the separating surface is of paramount importance. However, where this manifold lies is unknown. This is an important remark, because knowing its location and the current state of the system would allow to adequately estimate the effort to be taken to move the system into the right attraction basin. Fortunately, to address and solve this problem, numerical schemes based on reliable and up-to-dated state of the art algorithms have been recently developed to numerically reconstruct in an efficient, reliable and fast way the separatrix, (Cavoretto *et al.*, 2011, 2013, 2016a,b; De Rossi *et al.*, 2018; Franco *et al.*, 2016, 2017, 2018; Hilker *et al.*, 2017).

TABLE 3: STABILITY OF ALL THE EQUILIBRIA OF THE SYSTEM (2).

Equilibria	Stability conditions
$E_0 = (0, 0, 0)$	unstable
$E_N = (0, 0, H_N)$	unstable
$E_Q = (0, H_Q, 0)$	unstable
$E_P = (H_P, 0, 0)$	unstable
$E_{QN} = (0, Q^*, N^*)$	unstable
$E_{PN} = (P^*, 0, N^*)$	unstable
$E_{PQ} = (H_P, H_Q, 0)$	stable
$E_* = E_{PNH}$	(9), (13), (12)

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