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Abstract In this paper we focus on some important aspects of model building. The discussion specifically concerns the case of predator-prey interactions. We introduce here two models whose slight difference lies just in the way predators survive. In the former, they are taken to feed only on the modeled prey, i.e. to be specialist; in the second one, they are generalists, i.e. they can survive on other not explicitly modeled food resources.

But our main focus is on the prey, that may disappear due to the Allee effect, if reduced to very low numbers. On the other hand, they also exhibit herd behavior. Out main aim is the discussion of the issues of mathematical modeling of such situation. We show on this example that modeling requires much more than equations patching from different systems.

The analysis of the models indicates that the ecosystem may collapse in the case of specialist predators. If the predators have other feeding resources, they instead can thrive. Both types of models exhibit bistability between the prey-free state and coexistence.

Keywords: Allee effect; Herd behavior; Group defense; Predator-prey.
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1. Introduction

Population dynamics is one of the main fields in mathematical biology, [17], with applications in several diverse domains, ranging from the cellular level up to the interactions of the largest animals, and possibly including also the spread of epidemics. In this paper of methodological nature, we consider an example related only to predator-prey models, but the discussion could possibly be extended to other types of population interactions. We particularly focus on the situation in which prey, under the predators pressure, may experience extinction if reduced at low numbers, but they also gather in herds. In case of animals not living on the ground but in space, the model should suitably be modified, e.g. for schools, in the case of fishes, or swarms for insects. Further, recent work on trophic cascades in predator-prey ecosystems has been examined in [11,21], while experimental work on predator-prey systems dates back for instance to [20].

Incidentally, the concept of herding is clearly related to animal behavior, but it has also been used in several fields other than biology, for instance in finance, see e.g. [7,12,15,22], as well as in psychology and behavioral sciences, [13,23].

In interacting population theory, herding hinges on the remark that predation on a flock usually occurs by the predator selecting and chasing one of the closest individuals that are visible. Thus the latter generally belong to the boundary of the herd, [1]. Figure 1 tries to empasize this situation in the case of a herd of roughly square shape. The individuals that are visible from the exterior, where an individual predator would be, are those on a portion of the boundary or near it. If there are n^2 individuals in the square, those on the perimeter are roughly $4n$; equivalently, if the population of size P is uniformly distributed on the ground, the one on the perimeter is of size $4\sqrt{P}$. Figure 2 shows the case of a circular herd of radius r: the population occupies, i.e. is proportional to, the area $P \approx \pi r^2$; the perimeter in this case being $2\pi r$, by elimination of r we are lead to $2\sqrt{\pi}\sqrt{P}$ individuals on the circumference. In both cases, the individuals on the boundary are approximately $k\sqrt{P}$, for some suitable constant k. By possibly changing the value of k, $k\sqrt{P}$ is also the number of individuals that we expect to find on the boundary in the situation of the generic shape depicted in Figure 3. In the formulation of the model, mathematically this translates into remarking that the interaction term modeled as mass action, i.e. the direct product of the the prey and the predators populations, should be avoided. This assumption is instead reasonable with the classical predator-prey interactions where the prey live alone and predation involves one-to-one contacts between an individual predators and an individual prey.

The interaction term, must also be combined with a suitable reproduction function. There are several choices for the latter, and the purpose of this investigation is to discuss this issue in some very specific situations. The two classical ways of modeling the population growth are the Malthus model, which implies unbounded growth even in the presence of limited resources, and the Verhulst variation, which corrects this behavior via a logistic function. Another variant is represented by the
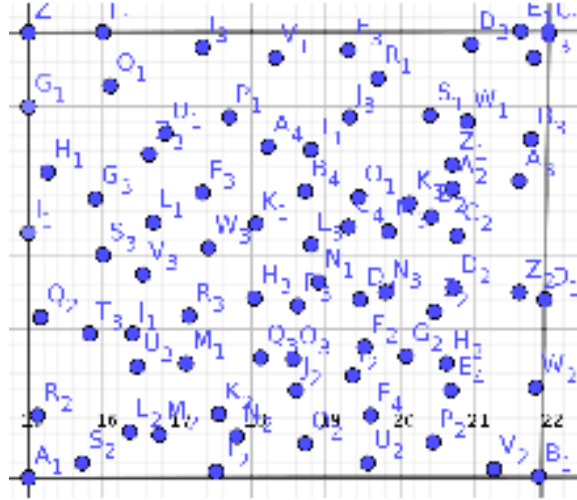
Fig. 1. A herd in the rough shape of a square. Each blue point represents an individual in the population. On the boudary we find roughly the square root of the total individuals in the area.
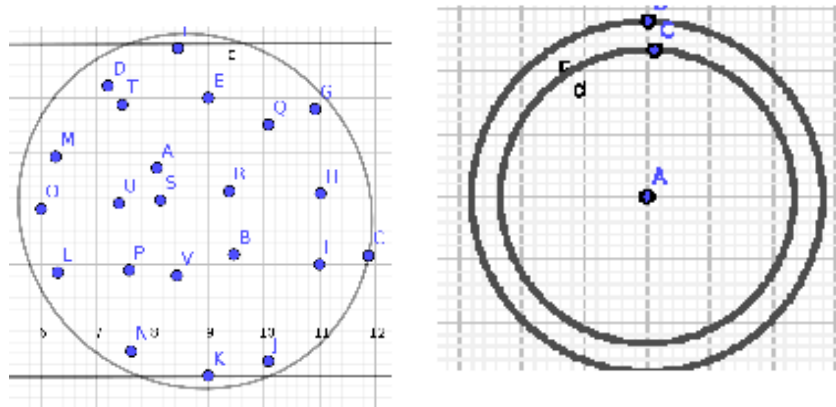

Fig. 2. The herd in a circular form. Left: the population in the circle; Right: the portion of the bounday subject to predators' attacks is contained between the two circles.

Holling types II (HTII) and III (HTIII) functions, which impose an upper bound on the intake of food for an individual in the unit of time, differing by their shape near the origin, i.e. for low population values, one such instance being discussed at
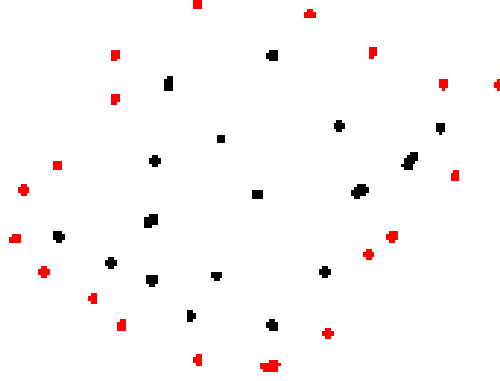
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Fig. 3. A generic shape of a herd of size P. Each point represents an individual in the population, those in red are the boundary individuals most affected by predators' attacks. Their number is approximately $k\sqrt{P}$, with k depending on the shape of the herd.

depth in [6].

Of particular interest here is a further variation, that was introduced by Allee, who hypothesized a negative growth for a population reduced to very low numbers, [2,3,16,10,19]. Our aim is the construction of a sound system that adequately contains both features illustrated above, the herd behavior and the Allee effect.

Section 2 is the main point of this paper, because we revisit the building of the interaction models. In Section 3 we reformulate them properly so as to accommodate the discrepancies that would arise with a simple-minded combination of some of the above formulations.

The specialist predator model is examined at first, in Section 4, assessing its equilibria and their stability and other related issues. Subsequently, the generalist predator case is considered in Section 5. A comparison of the possible outcomes of the two systems with the earlier papers concludes the paper.

Throughout the paper we assume that predators hunt individually. We also note that models for pack hunting are known in the literature, [9], as well as pack-and-herd behavior, or other kinds of interactions such as symbiosis or competition, [18]. In this latter case the phenomenon of tristability is discovered, allowing competing populations to thrive together for suitable initial conditions, in spite of the fact that for other starting points the principle of competitive exclusion still holds. However, in our approach we do not focus on these other possible issues, because,

as mentioned, here we take the models that follow as mere examples on which to discuss wider methodological issues.

2.   The incorrect model building process

In the presence of a reasonably large flock, the number of prey on its perimeter (a linear, one-dimensional manifold) is proportional to the square root of the total prey population (that occupies a bidimensional territory), originating the "square root" type of response, [1]. More generally, this functional form can be replaced by another exponent, say α, to accommodate for shapes of the herd that are not nice figures (e.g. possibly fractals), [8], and for the corresponding three-dimensional case. The latter, for smooth shapes of the fish schools or bird flocks, would instead correspond to the exponent $2/3$, the surface to volume ratio in three dimensions. Thus, if we denote by X and Y respectively the prey and predators populations, the hunting process in such case would generally be modeled via the term

$$YX^{\alpha}, \quad \frac{1}{2} \leq \alpha < 1. \tag{2.1}$$

Note that the individual behavior of the predators is reflected by the use of the exponent one of Y. Although pack predation could also be considered, it is not our concern here.

However, the problem which arises with the usual way of modeling herding consists in the fact that when the population contains just a few individuals, they cannot really constitute a herd. Thus, this feature fails when only a few prey are around, as remarked above, and therefore the square root functional form becomes inadequate. In the case of a low prey density indeed, even if gathering together, they do not form a herd in the proper sense, because all of them would be equally visible by the predators. Thus, in this circumstance, hunting becomes again a one-to-one affair as the classical predator-prey models in mathematical population biology state. As mentioned earlier, these are then modeled via the Holling type I (HTI), corresponding to mass action interactions , HTII or HTIII depending on the assumptions on feeding satiation, for instance. But note that in all these functions, there occurs always a bilinear term involving both prey and predators and no other powers of the prey population are employed.

A simple-minded approach for the formulation of a model combining a square root predation, describing predator interaction with a herd of prey, and also exhibiting the possibility of prey disappearance at very low numbers, i.e. the Allee effect, would consist in patching up the terms corresponding to these two cases. We describe the mathematical process in the next paragraphs.

In order to set up the system, we start from the prey X growth in a logistic fashion, with net reproduction rate r and carrying capacity K. However, to account for the fact that at low population values the prey are endangered, we introduce the Allee effect, with threshold c, below which the growth rate becomes negative.

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The threshold is sufficiently low so that the consistency condition is satisfied:

$$0 < c < K. \tag{2.2}$$

The prey equation for the Allee model would then be

$$X'(t) = rX\left(1 - \frac{X}{K}\right)(X - c). \tag{2.3}$$

The combination of (2.1) and (2.3) would then produce the prey following equation

$$X'(t) = rX\left(1 - \frac{X}{K}\right)(X - c) - aYX^{\alpha}. \tag{2.4}$$

This formulation appears to be mathematically correct, but it makes no sense. Indeed, for a large prey population, the first term in (2.4) does not differ much from the classical logistic formulation, so that the analysis would not differ much from the one of [1]. Instead, if X drops to low numbers, the Allee effect in the first term prevails, but the second one becomes absolutely unrealistic to describe the prey evolution. Indeed, as stated formerly, it implies prey herding, but the herd of a few individuals has the boundary coinciding with the whole set. The exponent $\alpha < 1$ therefore becomes inadequate to describe this situation, as the predators at this point see all individuals and can catch any one of them on a one-to-one basis. Hence, in this situation we should rather have $\alpha = 1$. We now correct this approach.

3. Proper functional response derivation

We need to better specialize the response function. It has to possess the features that when the prey are numerous, they gather in a flock and therefore mainly the ones on the perimeter are hunted, while if just a few, the predation must revert to the classical case of one-to-one interactions and be modeled again by a HTI term. Thus the function $\Phi(X)$ for large X should be asymptotic to $\sqrt{X}$, while for $X \to 0$ it should look like X. A function exhibiting these features has already been introduced in [5]:

$$\Phi(X) = \sqrt{X}(1 - e^{-\sqrt{X}}) \tag{3.1}$$

so that

$$\Phi(X) \approx X \ \ \text{for} \ \ x \to 0; \ \ \ \Phi(X) \approx \sqrt{X} \ \ \text{for} \ \ x \to \infty.$$

Figure 4 shows the differences of (3.1) with the Holling type I and the square root response functions: for X is near zero HTI and $\Phi(X)$ show little differences, for large X the function $\Phi(X)$ in (3.1) has large discrepancies with the HTI but is close to the square root.
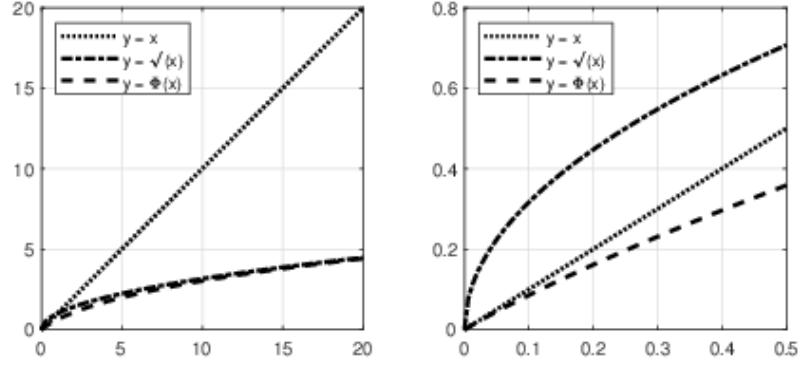
Fig. 4. A comparison between the graphs of $y = x$, $y = \sqrt{x}$ e $y = \Phi(x)$. Left: for large x the graph of $y = \Phi(x)$ resembles the graph of $y = \sqrt{x}$; Right: for small x it is similar to the one of $y = x$.

4.   Formulation of the model for the predators with no other food resources

We assume here that the predators Y are specialist on the prey modeled in the system, with mortality rate m, hunting rate a and conversion coefficient g. The prey is subject to the Allee effect. Its response function is taken in the form (3.1), so that we can write:

$$X'(t) = rX\left(1 - \frac{X}{K}\right)(X - c) - a\Phi(X)Y, \quad Y'(t) = ag\Phi(X)Y - mY. \quad (4.1)$$

The mathematical details of the analysis of (4.1) are deferred to Appendix 7. For this model, boundedness can be shown. We find the predator-free points $E_0 = (0, 0)$, the origin, corresponding to ecosystem collapse, $E_K = (K, 0)$, the equilibrium with prey at carrying capacity and $E_c = (c, 0)$, the threshold equilibrium. All these equilibria are unconditionally feasible. The origin turns out to be unconditionally stable, while the threshold is unconditionally unstable. For $E_K = (K, 0)$ the stability condition is

$$K < \Phi^{-1}\left(\frac{m}{ag}\right) = X^*. \quad (4.2)$$

Coexistence $E^* = (X^*, Y^*)$, is obtained in closed form as follows

$$X^* = \Phi^{-1}\left(\frac{m}{ag}\right), \quad Y^* = \frac{rg}{m}X^*\left(1 - \frac{X^*}{K}\right)(X^* - c). \quad (4.3)$$

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The feasibility condition for E^*:

$$c \leq \Phi^{-1}\left(\frac{m}{ag}\right) = X^* \leq K. \tag{4.4}$$

When E^* is feasible, E_c is an unstable node, while for E^* is unfeasible, E_c becomes a saddle. Thus, comparing (4.2) with (4.4), E_K is seen to be stable when E^* is unfeasible. This suggests the existence of a transcritical bifurcation for which coexistence emanates from the prey-only point when the prey population at coexistence increases past the carrying capacity.

Coexistence is stable if it lies sufficiently close to c, and unstable if it is close to K, namely $\mathrm{tr}(J)|_{E^*} < 0$ if and only if

$$c < X^* < z^*, \tag{4.5}$$

where z^* is given in Appendix 7. Further, a Hopf bifurcation may arise, with the onset of stable limit cycles, shown in Figure 5. The bifurcation diagram as function of predators mortality is given in Figure 6. The upper and lower curves indicate the maxima and minima of the oscillations.
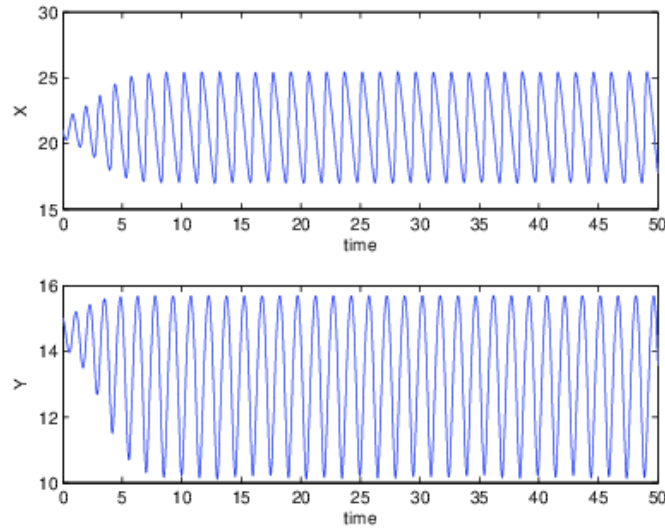

Fig. 5. Persistent oscillations obtained with the parameter values: $r = 2$, $K = 30$, $c = 10.5$, $a = 2$, $g = 1$, $m = 9.1$, $x_0 = 21$, $y_0 = 15$. Top the prey; Bottom the predators.

4.1. *The system behavior*

The origin is an attractor, and if E^* is unfeasible, E_K is stable. A stable manifold enters into the saddle E_c, partitioning the phase space into two basins of attraction,
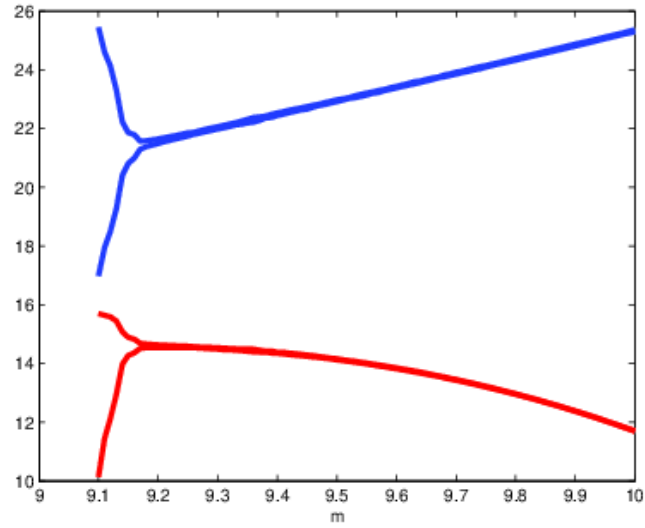
Fig. 6. Bifurcation diagram as function of m; Other parameter values: $r = 2$, $K = 30$, $c = 10.5$, $a = 2$, $g = 1$, $x_0 = 21$, $y_0 = 15$. In blue the prey, in red the predators. Hopf bifurcation at around $m \approx 9.2$. The upper and lower curves indicate the maxima and minima of the oscillations.

respectively for the origin and E_K.

When E^* is feasible, E_K becomes a saddle. In such case, E^* is an attractor, but the trajectories may also wind around the coexistence point and ultimately end at the origin, as shown in Figure 7.
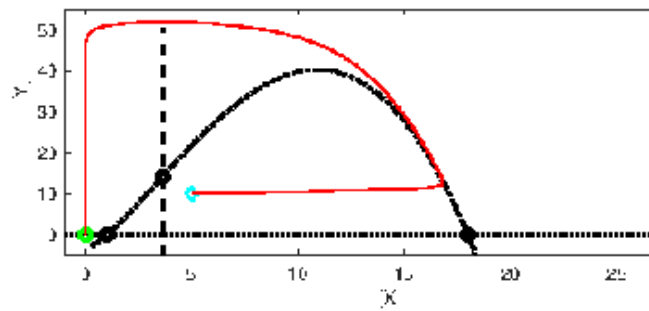

Fig. 7. The trajectory (red) in the prey-predator $X - Y$ phase space, for the initial values $X(0) = 5$ and $Y(0) = 10$ (light blue point), that approaches the origin, (green point). Parameter values $a = 1.4$, $g = 0.5$, $m = 1.6$, $r = 0.8$, $K = 10$, $c = 1$. Dashed-dotted: isocline $X' = 0$. Dashed: isocline $Y' = 0$. Dotted: the X axis.

5. The model formulation for predators feeding on external sources

For the mathematical details of this discussion, consult Appendix 8.

In this case we reformulate the predators dynamics allowing for a carrying capacity H due to the availability of alternative food supplies not explicitly modeled in the equations:

$$X'(t) = rX\left(1 - \frac{X}{K}\right)(X - c) - a\Phi(X)Y, \tag{5.1}$$

$$Y'(t) = ag\Phi(X)Y + sY\left(1 - \frac{Y}{H}\right).$$

Once again, this model has bounded trajectories. Its equilibria are the same as those of (4.1), but we also find the prey-free point $E_H = (0, H)$, which is unconditionally feasible. Coexistence equilibrium $E_* = (X_*, Y_*)$ differs, new different population values may arise, although they cannot be explicitly written.

While E_c retains its instability, also instability of the origin is now obtained. Here E_K is unconditionally unstable and E_H is instead always stable. In suitable conditions coexistence may again give rise to a Hopf bifurcation.

5.1. The system behavior

In this case, if coexistence is unfeasible, all the other equilibria on the prey axis being unstable, the trajectories must approach the prey-free state E_H. In such case this point is globally asymptotically stable. On the other hand, if coexistence is feasible, it will appear in pairs, $E_{*\pm}$. In this case there must be a heteroclinic trajectory joining the origin and E_{*-}, which is a saddle, defining the attraction basins of E_H and the one of E_{*+}, which instead should be a stable equilibrium.

Figure 8 shows the bifurcation diagram as function of the predators carrying capacity H. The transcritical bifurcation occurs at $H \approx 45$. When H grows past this value the coexistence equilibrium coalesces with E_H and the prey vanish.

6. Conclusion

The two models presented here exhibit both prey herd behavior and the Allee effect and differ on the feeding assumptions of the predators, whether they consume only this prey or capture also other not explicitly modeled food sources. Both systems ultimately share similar a behavior. Most importantly, the methodological approach to the modeling phase has been carefully elucidated so that the system does not contain incongruences.

The specialist predator case shows that bistability is possible, with both ecosystem exitinction and coexistence being possible system equilibria. In addition, a Hopf bifurcation occurs from coexistence, originating limit cycles. If coexistence becomes unfeasible, the ecosystem is doomed.
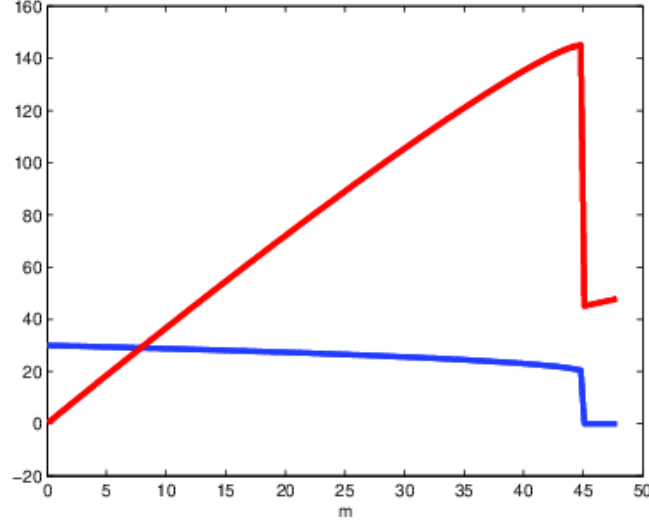
Fig. 8. Bifurcation diagram as function of H; Other parameter values: $r = 8$, $K = 30$, $c = 8$, $a = 1$, $g = 1$, $s = 2$, $x_0 = 21$, $y_0 = 15$. In blue the prey, in red the predators. The transcritical bifurcation occurs at $H \approx 45$.

For the generalist predators' case, again there are two basins of attraction, but in this case the outcome, other than coexistence, is the prey-free point.

The response function used for these models has already appeared in [5], where however the Allee effect is not present. Here we introduce it, suitably combining with prey herding. The results are similar with those of [5], but in addition incorporate the Allee effect, so that the prey vanish if they drop to too low population levels. If the predators are specialist, they disappear too, entailing ecosystem collapse, but if they can thrive on other food resources, they would survive at carrying capacity, with the prey become extinct.

7. Appendix A: The specialist predator model analysis

7.1. *Boundedness*

As long as the prey level at time t is $X(t) > K+1$, from the first equation in (4.1), $X'(t) < 0$. Thus the prey population decreases, and ultimately, for large t, we must have that the prey population is bounded, $X(t) < K+1$. Taking $W = gX + Y$ and

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differentiating, we obtain

$$W' = grX\left(1 - \frac{X}{K}\right)(X - c) - mY \leq M - m(W - gX)$$
$$= -mW + M + mgX \leq -mW + M + gm(1 + K),$$

where, over the interval $[0, K + 1]$, M denotes the maximum value of the cubic polynomial in X in the above formula. Thus $W'(t) < 0$ for $W > m^{-1}[M + (1 + K)gm]$. This implies that for large t we have the bound $W(t) < M + (1 + K)gm + 1$. Because W is bounded and both X and Y are nonnegative, they must be bounded as well.

7.2. *Equilibria*

In the predator's absence, we find the points $E_0 = (0, 0)$, the origin, corresponding to ecosystem collapse, $E_K = (K, 0)$, the predator-free point with prey at carrying capacity and $E_c = (c, 0)$, the threshold equilibrium. Here the prey have vanishing net reproduction and are on the verge of experiencing a negative growth rate, should their size decrease. All these points are unconditionally feasible, in the latter case recall anyhow the assumption (2.2).

For coexistence $E^* = (X^*, Y^*)$, from the second equilibrium equation of (4.1), observing that Φ is clearly invertibile, we obtain X^*. Upon substitution into the first equilibrium equation, produces the equilibrium value of the predators, giving in the end (4.3). Feasibility of this point depends only on the sign of the predators level Y^*, as the prey are unconditionally positive. Now, by using (2.2), the cubic on the right of (4.3) is easily seen to be positive only in the following interval which therefore gives (4.4).

7.3. *Stability*

The Jacobian of (4.1) is

$$J = \begin{bmatrix} -3\dfrac{r}{K}X^2 + 2r\left(1 + \dfrac{c}{K}\right)X - rc - a\Phi'(X)Y & -a\Phi(X) \\ ag\Phi'(X)Y & ag\Phi(X) - m \end{bmatrix}$$

Evaluation at the origin gives the eigenvalues $-rc$ and $-m$, which shows that it is unconditionally locally asymptotically stable.

At the point $E_c = (c, 0)$ we find instead the following eigenvalues, for one of which using (2.2) the sign can be assessed

$$rc\left(1 - \frac{c}{K}\right) > 0, \quad ag\Phi(c) - m$$

so that it is unconditionally unstable. Note that when E^* is feasible, E_c is an unstable node, because the Jacobian has two positive eigenvalues, compare the second one with (4.4), but when E^* is unfeasible, E_c becomes a saddle.

For $E_K = (K, 0)$ the eigenvalues are

$$-r(K - c) < 0, \quad ag\Phi(K) - m.$$

From the second one the stability condition (4.2) follows.

Applying the Routh-Hurwitz conditions to the coexistence equilibrium, one of them is seen to hold unconditionally,

$$\det(J) = ma\Phi'(X^*)Y^* > 0; \tag{7.1}$$

from (3.1), note indeed that

$$\Phi'(x) = \frac{1}{2\sqrt{x}}(1 - e^{-\sqrt{x}}) + \frac{1}{2}e^{-\sqrt{x}} > 0. \tag{7.2}$$

For the trace, we have

$$\mathrm{tr}(J)|_{E^*} = -3\frac{r}{K}X^{*2} + 2r\left(1 + \frac{c}{K}\right)X^* - rc - a\Phi'(X^*)Y^*.$$

To study this function, recalling (4.3), let us introduce the polynomials

$$q(x) = -3\frac{r}{K}x^2 + 2r\left(1 + \frac{c}{K}\right)x - rc,$$

$$p(x) = \frac{rg}{m}x\left(1 - \frac{x}{K}\right)(x - c)$$

so that we can write

$$\mathrm{tr}(J)|_{E^*} = q(X^*) - f(X^*), \quad f(x) = a\Phi'(x)p(x).$$

We need to assess when the condition $q(x) \leq f(x)$ holds. Now q is a quadratic with roots

$$x^+ = \frac{K + c}{3} + \sqrt{1 - \frac{c}{K} + \frac{c^2}{K^2}}, \quad x^- = \frac{K + c}{3} - \sqrt{1 - \frac{c}{K} + \frac{c^2}{K^2}}.$$

In view of (2.2), it is easily checked that

$$q(c) = rc\left(1 - \frac{c}{K}\right) > 0, \quad q(K) = -r(K - c) < 0,$$

so that q has a zero $x^+ \in (c, K)$ and

$$q(x) > 0, \quad x \in (c, x^+); \qquad q(x) < 0, \quad x \in (x^+, K). \tag{7.6}$$

On the other hand,

$$p(x) > 0, \quad x \in (c, K). \tag{7.7}$$

From (7.2), observe that

$$0 < \Phi'(x) < 1, \quad x > 0; \quad \Phi'(0) = 1; \quad \lim_{x \to +\infty} \Phi'(x) = 0. \tag{7.8}$$

Thus combining (7.7) and (7.8), we find

$$f(x) > 0, \quad x \in (c, K). \tag{7.9}$$

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From (7.9) and (7.6) it also follows that there is a point $z^* < x^+$ such that $f(z^*) = q(z^*)$, with $f(z) < q(z)$ for $z < z^*$ and $f(z) > q(z)$ when $z > z^*$, giving (4.5).

The result on the determinant, (7.1), combined with the one on the trace also indicates that when the latter vanishes, there occurs the onset of persistent oscillations.

8. Appendix B: The generalist predator model analysis

8.1. *Boundedness*

Here the result can be proved following the lines of Subsection 7.1. For large t, we again have that the prey population is bounded, $X(t) < K + 1$. Substituting into the second equation, we have

$$Y'(t) \leq ag\Phi(K+1)Y + sY\left(1 - \frac{Y}{H}\right).$$

If at some time $Y > H[1 + ags^{-1}\Phi(K+1)] + 1$, it follows $Y' < 0$, so that for large t we have $Y(t) < H[1 + ags^{-1}\Phi(K+1)] + 1 = L$. Hence the system's trajectories are confined in the box $[0, K+1] \times [0, L]$.

8.2. *Equilibria*

In the absence of the prey modeled in (5.1), the predators in this case settle to their carrying capacity H. Thus in addition to the predator-free equilibria of (4.1), here we have also the prey-free point $E_H = (0, H)$, which is unconditionally feasible. Only the coexistence equilibrium $E_* = (X_*, Y_*)$ needs to be investigated again, as it may differ from the former one found for (4.1).

Indeed we find coexistence by solving the predators' equilibrium equation, to find

$$Y = \frac{H}{s}\left[ag\Phi(X) + s\right] \tag{8.1}$$

and substituting into the prey one, we obtain the function

$$rX\left(1 - \frac{X}{K}\right)(X - c) - a\Phi(X)\left[\frac{H}{s}(ag\Phi(X) + s)\right] = 0$$

The equilibrium can be assessed by intersecting the curves

$$\phi(X) = rX\left(1 - \frac{X}{K}\right)(X - c), \quad \Psi(X) = a\Phi(X)\left[\frac{H}{s}(ag\Phi(X) + s)\right].$$

Now, ϕ has only a feasible convex branch in the interval $[c, K]$ and vanishes at the endpoints. Instead, $\Psi(0) = 0$ and $\Psi(X) \approx X$ as $X \to +\infty$. Recalling (7.2), the function $\Psi(X)$ is monotonically increasing. Therefore $\Psi(X)$ may or may not intersect $\phi(X)$, and if it does, it crosses it twice, say at the points $X_{*\pm}$, from which (8.1) provides the predators' values $Y_{*\pm}$.

8.3. *Stability*

In this case the Jacobian of (5.1) is

$$\widehat{J} = \begin{bmatrix} -3\dfrac{r}{K}X^2 + 2r\left(1+\dfrac{c}{K}\right)X - rc - a\Phi'(X)Y & -a\Phi(X) \\ ag\Phi'(X)Y & ag\Phi(X) + s - 2\dfrac{s}{H}Y \end{bmatrix}$$

Note that at the origin in this case we find the eigenvalues $-cr$ and $s > 0$, showing that it is a saddle, with the unstable manifold along the predator's axis.

At E_c the eigenvalues are $rc(1 - cK^{-1}) > 0$ as before and $ag\Phi(c) + s > 0$, which again show that it is unstable.

At E_K we find instead $-r(K - c) < 0$ and $ag\Phi(K) + s > 0$, implying in this case that it is unconditionally unstable.

The eigenvalues of $\widehat{J}$ evaluated at E_H are explicit, $-rc - aH < 0$, $-s < 0$ so that it is unconditionally stable.

For coexistence $E_{*\pm}$, the Routh-Hurwitz conditions become

$$-\operatorname{tr}(\widehat{J}|_{E_{*\pm}}) = 3\frac{r}{K}X_{*\pm}^2 - 2r\left(1+\frac{c}{K}\right)X_{*\pm} + rc + a\Phi'(X_{*\pm})Y_{*\pm} + \frac{s}{H}Y_{*\pm}, \tag{8.2}$$

$$\det(\widehat{J}|_{E_{*\pm}}) = a^2 gY_{*\pm}\Phi(X_{*\pm})\Phi'(X_{*\pm}) \tag{8.3}$$

$$-\frac{s}{H}Y_{*\pm}\left[-3\frac{r}{K}X_{*\pm}^2 + 2r\left(1+\frac{c}{K}\right)X_{*\pm} - rc - a\Phi'(X_{*\pm})Y_{*\pm}\right] \tag{8.4}$$

and both quantities must be positive to ensure stability.

Note that if the trace vanishes, the condition for the onset of a Hopf bifurcation requires a positive determinant and thus explicitly becomes:

$$a^2 g\Phi(X_{*\pm})\Phi'(X_{*\pm}) > \frac{s^2}{H^2}Y_{*\pm}. \tag{8.5}$$

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