Working Paper

Bifurcation Analysis of Two Predator-Prey Models

Alessandra Gragnani

IIASA

Bifurcation Analysis of Two Predator-Prey Models

Alessandra Gragnani

WP-94-65

August, 1994

ABSTRACT

Bifurcation analysis is used to systematically detect unrealistic dynamic behaviors of two predator-prey models that have recently received support and attention. Comparisons with other existing models are also made, in order to show that the singularities of the two examined models are due to some biological weakness of their functional forms.

BIFURCATION ANALYSIS OF TWO PREDATOR-PREY MODELS

Alessandra Gragnani

1. INTRODUCTION

During the last decades, a great number of predator-prey models have been proposed and used for descriptive and management purposes. Nowadays, it is clear that there is a need for serious analyses of all of these models, because many of them are somehow equivalent, while others are unreasonable from a biological point of view. In the first case, one should retain only one model (perhaps the most analytically tractable) for each equivalence class, while in the second case, one should simply disregard the model.

In a recent paper, Yodzis (1994) has pointed out how the analysis could proceed. First of all, before making any sort of computation, there should be a critical focus on the functional form of the model, in order to detect, a priori, if there is some biological weakness in the underlying assumptions. This is very clearly done by Yodzis in two cases: the model with predator interference applied by Hassel and Varley (1969) to parasitoids (recently supported by Arditi and co-workers (Arditi and Ginzburg (1989), Arditi and Akçakaya (1990), Arditi and Berryman (1991), Arditi et al. (1991a), Arditi et al. (1991b)) and the model proposed by Leslie (1948) and employed in a very influential paper by May et al. (1979) and later by Flaaten (1988) to typify the strategic approach to multispecies management.

The a priori analysis of a poor model is not always sufficient to identify its weaknesses, because bugs might be very difficult to find. Thus, a second step is needed, by means of which the bug can be detected, perhaps confirming some

doubts that emerge from an a priori analysis. For this, a formal analysis can be performed, in order to check, a posteriori, if the model can behave properly by suitably tuning its parameters. For example, in Yodzis (1994), the dependence of the equilibrium of the Leslie model upon the harvesting effort is computed and shown to be unreasonable from a biological point of view. This confirms, a posteriori, that such a model is not sound.

In order to detect singularities and weaknesses of a model, a very general and classical approach is followed in this paper: namely, bifurcation analysis. In the ecological context, this approach was pioneered by Bazykin (1985), who analyzed and compared a great number of models of interacting populations. In the next section, the bifurcation analysis of an extended version of Leslie's model is performed and it is shown that tangent bifurcations of cycles may arise. This means that such a model can have, for a given parameter setting, two alternative attractors (an equilibrium and a limit cycle). This is a real surprise, because standard predator-prey communities have only one attractor, as pointed out by May (1976), who, by the way, considered this model in some detail without noticing its singularity. This finding reinforces the criticism of Yodzis (1994) of Leslie's assumption (logistic predator with carrying capacity proportional to prey density). Then, in Sect. 3, a model with predator interference is studied and it is shown that, indeed, this model has a very particular mode of behavior, called tangle. Moreover, it is demonstrated that the tangle can not be present if a particular pathology of the functional response is removed.

2. THE LESLIE-HOLLING MODEL

In the predator-prey model originally formulated by Leslie (1948), the prey is logistic, the functional response of the predator is linear and the predator is

2

logistic, with carrying capacity proportional to prey density. In Yodzis (1994), this model is criticized and shown to be "not easily defensible" from a biological point of view. Here a slightly more complex model, called the Leslie-Holling model (because the predator has a Holling type II functional response (Holling (1965)), is considered. Thus, the model is the following

$$\dot{x} = r x \left(1 - \frac{x}{K}\right) - \frac{a x}{b + x} y \qquad (1a)$$

$$\dot{y} = s y \left(1 - \frac{y}{h x}\right) \qquad (1b)$$

where x and y are indicators of abundance of prey and predator, and r, K, a, b, s and h are positive and constant parameters.

Both models have one, and only one, strictly positive equilibrium for any parameter setting, but in the Leslie model this equilibrium is always asymptotically stable, so that there are no limit cycles, while in the Leslie-Holling model the equilibrium can be unstable and surrounded by a stable limit cycle, as noticed by May (1976). In this respect the Leslie-Holling model seems to be similar to the most famous and most often used predator-prey model

$$\dot{x} = r x \left(1 - \frac{x}{K}\right) - \frac{a x}{b + x} y \qquad (2a)$$

$$\dot{y} = e \frac{a x}{b + x} y - d y \qquad (2b)$$

sometimes called the Rosenzweig-McArthur model, in recognition of their pioneering work (Rosenzweig and McArthur (1963)). (See also: Rosenzweig (1971), Gilpin (1972), May (1972), Shimazu et al. (1972), Hsu et al. (1978)). Model (1) is very often used by practitioners because logistic growth and type II functional response are well established notions. It is sometimes preferred to the Rosenzweig-McArthur model because its limit cycle (when it exists) is not stuck on the x, y axis as the limit cycle of model (2). The Leslie-Holling predator

equation (1b) coincides with that of the Leslie model, so that the criticisms raised by Yodzis to this equation also apply in the present case. The critique can be summarized by noting that the predator described by equation (1b) can live forever on arbitrarily small amounts of resource, indeed, a biological absurdity.

It is now shown, by means of standard bifurcation analysis, that model (1) has an unexpected and unsound dynamic behavior for some parameter values. In other words, the pathology of the functional form of the model gives rise to pathological dynamics.

Model (1) has the general form of positive dynamical systems

$$\dot{x} = x f(x, y)$$
$$\dot{y} = y g(x, y)$$

and for any parameter setting there exists one, and only one, strictly positive equilibrium (x^+, y^+) given by

$$x^+ = \frac{-(ahK - rK + rb) + \sqrt{(ahK - rK + rb)^2 + 4r^2 Kb}}{2r} \qquad (3a)$$

$$y^+ = hx^+ \qquad (3b)$$

The Jacobian matrix J evaluated at (x^+, y^+), i.e.,

$$J = \begin{bmatrix} x^+ f_x & x^+ f_y \\ y^+ g_x & y^+ g_y \end{bmatrix}$$

can then be easily computed. By annihilating the trace of J, the explicit relationship among the parameters that characterize a Hopf bifurcation can be found, provided the determinant of J is positive (Guckenheimer and Holmes (1983)). Such a condition is

$$2rx^{+^2} + x^+(rb - rK + sK) + sKb = 0 \qquad (4)$$

4

where x^+ is given by (3a). Equations (3a) and (4) allow the determination of Hopf bifurcation curves in any two-dimensional parameter space. Fig. 4.2 at page 54 of May (1976) shows one example of such a curve. Another example is shown in Fig. 1a, where the Hopf bifurcation curve is drawn in the parameter space (a,K) for the parameter values specified in the caption. The figure shows that the Hopf bifurcation curve is split into two parts. The first, H^-, is a supercritical Hopf bifurcation: crossing this curve from region 1 to region 2 the equilibrium (x^+,y^+) becomes unstable and surrounded by a stable limit cycle that is initially very small. The second, H^+, is a subcritical Hopf bifurcation: crossing this curve from region 2 to region 3, the unstable equilibrium (x^+,y^+) becomes stable and is surrounded by an unstable limit cycle. Thus, just below the curve H^+ in region 3, the system has two limit cycles around the stable equilibrium (x^+,y^+): the internal cycle is unstable while the external cycle is stable. Fig.1b shows this situation: trajectories starting inside the unstable limit cycle tend towards equilibrium, while trajectories starting outside tend towards the stable limit cycle. Since in region 1 the two cycles do not exist, there must be a line, rooted at point Z, on which the two cycles disappear. This is the tangent bifurcation curve T: coming from above, the two cycles collide on this curve and disappear.

The point Z, where the three bifurcation curves H^-, H^+ and T are rooted, can be determined by finding the point on the Hopf bifurcation curve where the so-called Liapunov number is annihilated (Guckenheimer and Holmes (1983)). In the present case, this has been done by means of a standard package for algebraic manipulation. Then, starting from point Z, the tangent bifurcation curve has been obtained by means of LOCBIF, a specialized program implementing an adaptive continuation procedure for bifurcation analysis (Khibnik et al. (1993)).

The existence of a zero Liapunov number, i.e., the possibility of having two distinct stable modes of behavior (see Fig.1b), is not consistent with the premises. In fact, the model pretends to describe the simplest case of interactions between a prey and a predator and in such a framework alternative attractors can hardly be imagined (May (1976)). On the contrary, it is known that a predator-prey model can have multiple attractors if the predator is harvested by a Holling type II superpredator (Muratori and Rinaldi (1989)). But in no way, not even in an approximate or weak sense, eq. (1b) can interpret the dynamics of such an exploited population.

3. THE HASSEL - VARLEY MODEL

The best known formulation of the influence of predator interference on functional response is that of Hassel and Varley (1969). The corresponding predator-prey model, here called Hassel-Varley model, is (in the simplest formulation) the following:

$$\dot{x} = r x \left(1 - \frac{x}{K}\right) - \frac{a\,x}{\beta y + x} y \tag{5a}$$

$$\dot{y} = e \frac{ax}{\beta y + x} y - dy \tag{5b}$$

From a formal point of view, this model looks very similar to the much more known and applied Rosenzweig-McArthur model (2). Indeed, the only difference is that the parameter b in (2) is replaced by βy in (5). Such a term (βy or b) is proportional to the so-called searching time of the predator, namely, the time spent by each predator to find one prey. Thus, in the Rosenzweig-McArthur model the searching time is assumed to be independent of predator density, while in the Hassel-Varley formulation the searching time is proportional to predator

density (i.e., predators strongly interfere). Different (but equivalent) interpretations of the parameter β have been suggested by Arditi and co-workers in a series of papers dealing with ratio-dependent predators (Arditi and Ginzburg (1989), Arditi and Akçakaya (1990), Arditi and Berryman (1991), Arditi et al. (1991 a), Arditi et al. (1991b)).

Although the Hassel-Varley model is quite convenient for data analysis and for sensitivity analysis of the equilibrium (see above mentioned papers by Arditi and co-workers) it contains (as remarked by Yodzis (1994)) a biologically unreasonable assumption, namely that the searching time of the predator tends to zero when the predator density tends to zero. Obviously, this has no serious consequences if the model is used to interpret field and laboratory data collected during periods of relatively high abundance of predator. On the contrary, this assumption might have pathological consequences on the dynamic behavior of the model as shown below through bifurcation analysis.

It is easy to check (for example, by drawing isoclines) that model (5) has always two trivial equilibria $((x,y)=(0,0);\ (x,y)=(K,0))$ and at most one strictly positive equilibrium (x^+,y^+) given by

$$x^+ = \frac{K}{\beta e r}\left[e(\beta r - a) + d\right] \tag{6a}$$

$$y^+ = \frac{ea - d}{\beta d}x^+ \tag{6b}$$

For $(ea\text{-}d)$ tending to zero, y^+ tends to zero and the strictly positive equilibrium (x^+,y^+) collides with the trivial equilibrium $(K,0)$, so that

$$ea\text{-}d=0$$

is a bifurcation (transcritical bifurcation). The equilibrium (x^+,y^+) can be either stable or unstable and the two situations are separated by a Hopf bifurcation, which can be detected by annihilating the trace of the Jacobian, thus obtaining

$$e^2 a(a - \beta r) - de\beta(ea - d) - d^2 = 0 \qquad\qquad (7)$$

which is easy to check. The associated Liapunov number, computed with software for algebraic manipulation, turns out to be very complex. It is, therefore, practically impossible to formally prove that the Liapunov number is always negative, i.e., that the Hopf bifurcation is always supercritical. Nevertheless, a huge number of randomly generated numerical tests on the sign of the Liapunov number, and a greater number of simulations of model (5) allow a strong conjecture that the Hopf bifurcation is always supercritical. This means that this model is, as far as the Hopf bifurcation is concerned, similar to the Rosenzweig-McArthur model, for which the Hopf bifurcation has been proved to be supercritical by Sarkar et al. (1991). In conclusion, the model cannot have the two alternative attractors shown in Fig. 1b. This situation is summarized in Fig. 2a, where the Hopf bifurcation curve (see (7)) is drawn in the parameter space (e,a) for the parameter values reported in the caption. In region 1 all trajectories tend towards the strictly positive equilibrium (x^+, y^+), while in region 2 such equilibrium is unstable and trajectories tend towards a limit cycle.

By "continuing" the limit cycle in region 2 of parameter space, it is easy to verify that the period of the limit cycle is very sensitive to the parameters and becomes very large when approaching a heteroclinic bifurcation curve. In addition, the limit cycle becomes quite peculiar when this curve is approached: it passes closer and closer to the two trivial equilibria $(0,0)$ and $(K,0)$, and this is why the period of the limit cycle increases so much. The reason for this is that the strictly positive equilibrium (x^+, y^+) tends towards the origin when the parameters (e,a) tend towards the heteroclinic bifurcation curve, thus forcing the limit cycle (which surrounds the equilibrium (x^+, y^+)) to pass very close to the origin. The heteroclinic bifurcation curve is, therefore, the combination of

8

parameter values at which the equilibrium (x^+, y^+) collides with the origin and is identified (see (6)) by

$$e(\beta r - a) + d = 0 \qquad (8)$$

This bifurcation is very particular: not only does it correspond to the collision of two equilibria $((0,0)$ and $(x^+, y^+))$ but can also be viewed as the appearance of a kind of heteroclinic connection (i.e., a trajectoriy connecting two saddles). Indeed, for small positive values of $e(\beta r - a) + d$, the unstable manifold of the saddle $(K,0)$ tends to the limit cycle or to (x^+, y^+), and therefore comes very close to the saddle $(0,0)$, while for $e(\beta r - a) + d = 0$ it tends towards the origin. Nevertheless, for $e(\beta r - a) + d \leq 0$ the origin is no longer a saddle. This can be proved by studying the sign of $dy / dx = \dot{y} / \dot{x}$ in the vicinity of the origin. From eq. (5), neglecting higher order terms,

$$\frac{\dot{y}}{\dot{x}} = \frac{y}{x} \frac{(ea - d)x - \beta dy}{rx + (\beta r - a)y}$$

is obtained, and the function on the right-hand side is positive close to the x and y axis because condition $e(\beta r - a) + d \leq 0$ implies $ea - d > 0$ and $\beta r - a < 0$. This means that the origin is not a saddle, because otherwise $\dot{y} / \dot{x}$ would be negative everywhere. The state portraits in region 3 (i.e., for $e(\beta r - a) + d < 0$) are like those in Fig. 2b, which corresponds to point P in Fig.2a. All trajectories inside the region delimited by the stable and unstable manifolds of the saddle $(K,0)$ tend towards the origin for t→ ∞ and for t→ - ∞, while all other trajectories tend towards the origin for t→ ∞. This means that the origin is a global attractor (although it is an unstable equilibrium in the sense of Liapunov). Such an attractor is called tangle. Biologically, the tangle of Fig. 2b makes absolutely no sense; it says that both predator and prey become extinct no matter what initial conditions are, while any reasonable model should predict that the prey tends

towards its carrying capacity if the predator becomes extinct. Surprisingly, Arditi and Berryman (1991) interpret this unusual attractor by saying that it explains "repeated quasi-extinctions experienced by populations" (!?). On the contrary, they should have concluded that the model is meaningless, at least when it gives rise to the tangle.

It is interesting to note that the absurd behavior already pointed out disappears as soon as the model is corrected by introducing a base component ε to the searching time of the predator. Thus model (5) becomes

$$\dot{x} = r x \left(1 - \frac{x}{K}\right) - \frac{a x}{\varepsilon + \beta y + x} y \qquad (9a)$$

$$\dot{y} = e \frac{ax}{\varepsilon + \beta y + x} y - dy \qquad (9b)$$

where ε is small if interference is relevant. This model, proposed for different reasons by Beddington (1975) and De Angelis et al. (1975), cannot have a tangle, because close to the origin the system is described by $\dot{x} = rx$, $\dot{y} = -dy$, which are the equations of a saddle. This means that model (9) has only transcritical and Hopf bifurcations, just like the Rosenzweig-McArthur model (2). In other words, model (5) is not "robust", since even a small perturbation (the introduction of a small ε) destroys one of its possible modes of behavior, namely the tangle.

4. CONCLUDING REMARKS

This paper demonstrates how bifurcation analysis can be systematically used to discover weaknesses of a predator-prey model. The method has been applied to two models (Leslie-Holling (eq. (1)) and Hassel-Varley (eq. (5))), which have received, even recently, support and attention. The determination of the bifurcations of the models has allowed the discovery of hidden niches in

parameter space (see region 3 in Fig. 1a and 2a), where the dynamic behavior of the system is biologically absurd (multiple attractors in the first case (Fig. 1b), and extinction of both prey and predator in the second (Fig. 2b)). This agrees completely with the criticisms recently raised by Yodzis (1994) to these and analogous models.

The comparisons of the bifurcations of the Leslie-Holling model (1) with those of the Rosenzweig-McArthur model (2), have led to the conclusion that the second model should definitely be preferred to the first one. This suggestion should be followed, in particular, when the model is used to derive general theories or to build up larger models (e.g., food chains), or to interpret the role of seasons in predator-prey communities (see, for example, Hanski et al. (1993)). Similar comparisons have also been performed for the Hassel-Varley model (5), used by Arditi and co-workers, and for model (9), used by Beddington (1975) and De Angelis et al. (1975) many years ago. Model (9) has the same bifurcation structure as the Rosenzweig-McArthur model (2) and can certainly fit field data and support meaningful theories, at least as well as model (5). Moreover, it cannot produce unrealistic modes of behavior, such as the tangle depicted in Fig 2b, which, on the contrary, characterizes model (5). Therefore, model (9) should be preferred to model (5) when dealing with predators with relevant interference.

REFERENCES

Arditi, R. and Akçakaya, H. R. (1990). Underestimation of mutual interference of predators, *Oecologia*, 83, 358-361.

Arditi, R. and Berryman, A. A. (1991). The biological control paradox, *TREE*, 6, 32.

Arditi, R. and Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: ratio-dependence, *Journal of Theoretical Biology*, 139, 311-326.

Arditi, R., Ginzburg, L. R. and Akçakaya, H. R. (1991a). Variation in plankton densities among lakes: a case for ratio-dependence predation models, *The American Naturalist*, 138, 1287-1296.

Arditi, R., Perrin, N. and Saïah, H. (1991b). Functional responses and heterogeneities: an experimental test with cladocerans, *Oikos*, 60, 69-75.

Bazykin, A. D. (1985). *Mathematical Biophysics of Interacting Populations*, Nauka, Moscow, [in Russian].

Beddington, J. R. (1975). Mutual interference between parasites of predators and its effect on searching efficiency, *Journal of Animal Ecology*, 44, 331-340.

De Angelis, D. L., Goldstein, R. A. and O'Neill, R. V. (1975). A model for trophic interaction, *Ecology*, 56, 881-892.

Flaaten, O. (1988). *The Economics of Multispecies Harvesting*, Springer-Verlag, Berlin.

Gilpin, M. E. (1972). Enriched predator-prey systems: theoretical stability, *Science*, 177, 902-904.

Guckenheimer, J. and Holmes, P. (1983). *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields*, Springer Verlag, New York, Heidelberg, Berlin, Tokyo.

Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos, *Nature*, 364, 232-235.

Hassel, M. P. and Varley, G. C. (1969). New inductive population model for insects parasites and its bearing on biological control, *Nature*, 233, 1133-1136.

Holling, C. S. (1965). The functional response of predators to prey density, *Memoirs of the Entomological Society of Canada*, 45, 5-60.

Hsu,S. B., Hubbel, S. P. and Waltman, P. (1978). A contribution to the theory of competing predators. *Ecological Modelling*, 48, 337-349.

Khibnik, A. I., Kuznetsov, Yu. A., Levitin, V.V., Nikolaev, E. V. (1993), Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps, *Physica D*, 62, 360-370.

Leslie, H. P. (1948). Some further notes on the use of matrices in population mathematics, *Biometrika*, 35, 213-245.

May, R. M. (1972). Limit cycles in predator-prey communities, *Science*, 177, 900-902.

May, R. M. (1976). *Theoretical Ecology, Principles and Applications*, Blackwell Scientific Publications, Oxford, London, Edimburgh, Melbourne.

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J. and Laws, R. M. (1979). Management of multispecies fisheries, *Science*, 205, 267-277.

Muratori, S. and Rinaldi, S. (1989). A dynamical system with Hopf bifurcations and catastrophes, *Applied Mathematics and Computation*, 29, 1-15.

Rosenzweig, M. L. and McArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions, *The American Naturalist*, 97, 209-223.

Rosenzweig, M. L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time, *Science*, 171, 385-387.

Sarkar, A. K., Mitra, D., Ray, S. and Roy, A. B. (1991). Permanence and oscillatory co-existence of a detritus-based prey-predator model, *Ecological Modelling*, 53, 147-156.

Yodzis, P. (1994). Predator-prey theory and management of multispecies fisheries, *Ecological Applications*, 4(1), 51-58.
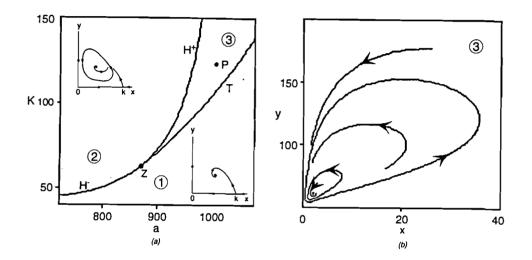
Fig. 1 The Leslie-Holling model: (a) Hopf and tangent bifurcation curves in the parameter space (a, K); (b) trajectories of the system corresponding to point P in region 3 (the values of the parameters are $r=5.4$, $s=2.8$, $b=2$, $h=0.01$, $a=1000$, $K=120$).
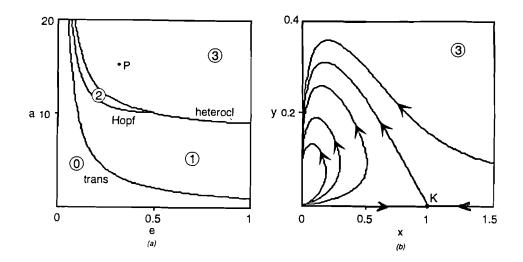
Fig. 2 The Hassel-Varley model: (a) transcritical, Hopf and heteroclinic bifurcation
curves in the parameter space (e,a); (b) trajectories of the system (tangle)
corresponding to point P in region 3 (the values of the parameters are $r=4$,
$K=1$, $e=0.3$, $a=15$, $\beta=2$, $d=1$).