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Limit Cycles in Predator-Prey Communities

Abstract. *Essentially all models that have been proposed for predator-prey systems are shown to possess either a stable point equilibrium or a stable limit cycle. This stable limit cycle, an explicitly nonlinear feature, is commonly overlooked in conventional analyses of these models. Such a stable limit cycle provides a satisfying explanation for those animal communities in which populations are observed to oscillate in a rather reproducible periodic manner.*

The dynamics of a community comprising populations of various interacting species may, in general, be modeled by a nonlinear set of differential equations. Consequently, the equilibrium or steady-state system need not necessarily be a set of constant time-independent populations (that is, a point equilibrium such as the equilibrium of a marble in the bottom of a cup) as it must be for a linear system, but can alternatively be a stable limit cycle wherein the population numbers undergo well-defined cyclic changes in time. The amplitude of such a limit cycle, that is, the maximum and minimum values the individual populations reach during the cycle, is fixed solely by the intrinsic parameters of the model such as birth rates, predation rates, and so on. For a stable limit cycle, just as for a stable point equilibrium, the system, if disturbed, will tend to return to the equilibrium configuration. This is illustrated in Fig. 1.

In this report I consider the wide class of models which have been proposed in the ecological literature for predator-prey systems. These models, the mathematical structures of which have increasingly been guided by field and laboratory observations, incorporate a variety of forms for the stabilizing density-dependent or resource-limitation effects in the prey birth rate, and the destabilizing functional and numerical responses (*1*) on the predators' behalf (corresponding to saturation of their appetites and reproductive capacities, and like effects). Working with the full nonlinear equations, I show here that essentially all such models possess either a stable equilibrium point or a stable limit cycle.

This rather robust theorem strongly suggests that those natural ecosystems which seem to exhibit a persistent pattern of reasonably regular oscillations (*2*) are in fact stable limit cycles. This interpretation is altogether different from the widespread explanation that such phenomena are associated with the oscillations in the unrealistically special neutrally stable Lotka-Volterra system (the stability of the frictionless pendulum), where the amplitude of oscillation depends wholly on the initial conditions (on how the pendulum was set swinging).

The limit cycle is a familiar phenomenon in other areas of theoretical biology (*3*), and the Kolmogorov theorem invoked below has recently been reviewed in ecological contexts (*4*). What is new in this report is the proof that such limit cycle behavior is implicit in essentially all conventional predator-prey models.

For a community comprising one prey species and one predator species, whose populations at time t are $x(t)$ and $y(t)$, respectively, a general model for the dynamics of the system may be written

$$dx/dt = x \; g(x,y) \qquad (1a)$$

$$dy/dt = y \; h(x,y) \qquad (1b)$$

where g and h are some arbitrary functions of x and y. A typical example from the ecological literature (*5*) is the pair of equations

$$dx/dt = rx(1-x/K) - ky(1-e^{-cx}) \qquad (2a)$$

$$dy/dt = -by + \beta y\,(1 - e^{-fx}) \qquad (2b)$$

The rate constants and other parameters in this particular pair of equations are as defined in (*5*) and elsewhere. The first term on the right-hand side in Eq. 2a is the prey birth rate, which includes a stabilizing density-dependent factor of the conventional logistic type. Were there no predators present, this factor would lead to a stable equilibrium point at $x = K$. Alternative expressions for the prey birth rate which are similar in effect, if different in detail, have been developed by Gompertz (*6*) [$rx \ln (K/x)$], Rosenzweig (*5*) $\{Rx^{1-a}[1-(x/K)^a]$, with $1 > a > 0\}$, and others (*7, 8*). The second term on the right in Eq. 2a represents the prey loss rate due to predation, of the form suggested on empirical grounds by Ivlev (*9*). This predation rate is proportional to x for small x, but saturates to a constant k for large x, this being a destabilizing element of the overall system. Other qualitatively similar forms have been developed by Gause (*10*) ($kx^{1/2}y$), Rosenzweig (*5*) ($kx^{\gamma}y$, with $1 > \gamma > 0$), Holling (*11*) [$kxy/(1 + cx)$], and others (*12, 13*). Similarly the second term on the right in Eq. 2b describes the relation between prey abundance and predator birth rate (Holling's numerical response), and may have either the explicit form given here or other equivalent forms (*12, 13*). The form of many of these interaction terms [particularly those in the work of Watt (*8, 12*) and Holling (*1, 11*)] is motivated by the observed properties of real predator-prey communities.

The familiar Lotka-Volterra system corresponds to the singular limiting case obtained by the use of greatly simplified forms for all terms in Eqs. 2a and 2b, namely, $K \to \infty$, $c \to 0$ with ck = constant, $f \to 0$ with $f\beta$ = constant. The consequent equation has purely neutral stability. Prey and predator populations will oscillate, with their amplitudes dependent entirely on how the system started off; if disturbed, the system will oscillate with some new amplitude; and so on. This is a most fragile result, and the slightest departure from the Lotka-Volterra form, for example, K not infinite, will destroy the neutral stability property.

In systems such as those represented by Eqs. 2a and 2b there is a tension between the stabilizing resource-limitation term and the destabilizing functional and numerical response terms. In conventional analyses of such models, either by analytical (*14*) or graphical (*15*) means, the potential equilibrium populations (that is, the points where $dx/dt = dy/dt = 0$) are found first, and then the outcome of this tension between stabilizing and destabilizing influences is studied in an infinitesimal neighborhood about this point. If the outcome of this linearized stability analysis is a stable equilibrium point, the system is regarded as stable; if the outcome is an unstable point, the system is regarded as transient, with one or more species being eliminated.

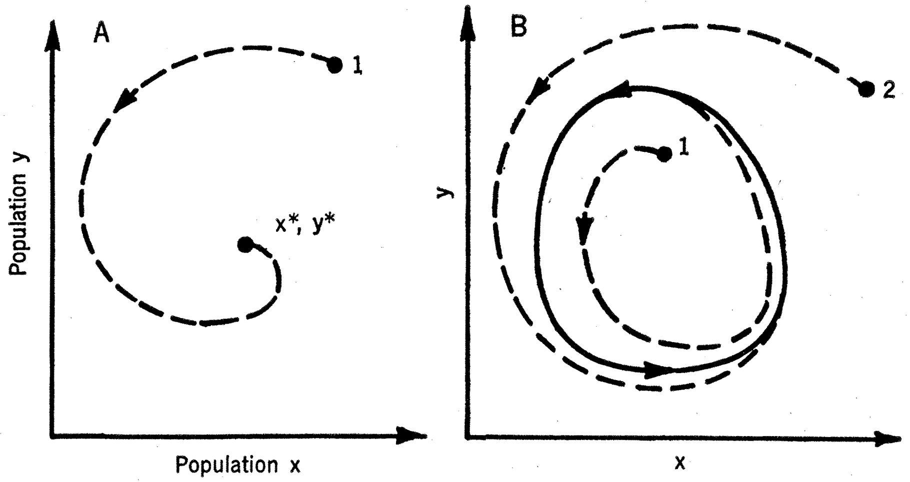

Fig. 1. Depiction of the "phase space" of two species, with populations x and y; each point in the plane corresponds to some particular value of the two populations. In (A) the point x^*, y^* is a stable equilibrium point; if the populations are displaced from it (for example, to point 1), they tend in time to return, as exemplified by the dashed line. In (B) the solid curve is a stable limit cycle, and in equilibrium the two populations cycle around and around this trajectory, exhibiting well-defined and periodic oscillations in the population numbers; if displaced, either inside (for example, to point 1) or outside (for example, to point 2) their stable limit cycle, they tend to return to it, as illustrated by the dashed lines.

However, there is a significant, and much neglected, theorem of Kolmogorov (*16*) which tells us that such models possess either a stable equilibrium point or a stable limit cycle. Kolmogorov first proved this theorem in a general predator-prey context, but its specific applicability to the conventional models catalogued above seems to have been overlooked. Thus those models which are discarded as "unstable" in fact achieve a stable cyclic oscillation in population numbers, between limits set not by the initial perturbations but by the model parameters themselves.

Kolmogorov's theorem may be applied to any equation of the form of Eqs. 1a and 1b where g and h are continuous functions of x and y, with continuous first derivatives. Clearly in a biological situation we deal only with populations $x \geqq 0$, $y \geqq 0$. The theorem then holds if the functions g and h have the following properties (*17*):

$$\partial g/\partial y < 0; \quad x\ \partial g/\partial x + y\ \partial g/\partial y < 0 \qquad (3)$$

$$\partial h/\partial y < 0; \quad x\ \partial h/\partial x + y\ \partial h/\partial y > 0 \qquad (4)$$

$$g(0,0) > 0 \qquad (5)$$

Also there exist A, B, C such that

$$g(0,A) = 0, \ A > 0 \qquad (6)$$

$$g(B,0) = 0, \ B > 0 \qquad (7)$$

$$h(C,0) = 0, \ C > 0 \qquad (8)$$

$$B > C \qquad (9)$$

Applying this theorem to the specific example given by Eqs. 2a and 2b, one can see that the mathematical condition given by Eq. 9 corresponds to the eminently reasonable biological assumption that the prey population for the (possibly unstable) predator-prey equilibrium point is smaller than that supportable by the environmental resources in the absence of predators. Explicitly, Eq. 9 requires

$$Kf > \ln\left[\beta/(\beta - b)\right]$$

which is naturally fulfilled in any sensible model. The remaining conditions given by Eqs. 3 through 8 are easily seen to be satisfied by the model given by Eqs. 2a and 2b.

The other forms for the prey birth rate and for the predator functional and numerical responses, referred to above, are qualitatively similar to those in the explicit example, and may readily be seen also to comply with the criteria given in Eqs. 3 through 9. The claim that this wide class of models has either a stable point equilibrium or a stable limit cycle is thus established (*18*). Insofar as the conventional predator-prey models catalogued above are realistic descriptions of natural communities, limit cycles are seen to be a common property of predator-prey ecosystems.

The fact that systems, which in a linearized stability analysis are classed as "unstable," may wind out to a stable limit cycle is easily overlooked in computer realizations of the models, because in most cases the ratio between the predator's minimum population and the predator's mean population in the limit cycle is roughly of the order (*19*)

$$\frac{y\ (\mathrm{min})}{y\ (\mathrm{mean})} \sim \exp\left[-\alpha\left(\frac{K}{x^*}\right)^2\right] \qquad (10)$$

Here α is a number of the order of unity, x^* is the mean prey population, and K is the maximum prey population capable of being sustained by the environmental resources: the essential assumption underlying Eq. 10 is that K/x^* is large. Since in typical computer models (*20*) $(K/x^*)^2$ is indeed substantially greater than unity, the ratio given in Eq. 10 is usually so small that the predator population is below unity, and therefore extinct, before the minimum of the limit cycle is reached. Indeed, so long as the cycle is severe enough to produce very low numbers of either predator or prey, stochastic features of the kind discussed by Bartlett (*21*) will enter and extinction will occur sooner or later. In short, the stable limit cycle may often be of no practical relevance. This question is one that depends on the numerical details of the parameters in a particular model.

The theorem presented here is likely to have implications for those natural systems in which the populations seem to increase and decrease in a rather stable periodic manner. Admittedly some of the population cycles reported in the literature are artifacts of the smoothing procedure employed in processing the data (*22*), but others are not. One may expect these genuine cycles to be stable limit cycles, sometimes with environmental fluctuations superimposed, between well-defined limits set by interspecific and intraspecific interactions.

For example, Lack (*23*) has suggested that the population cycles of lemmings in northern regions are the result of some predator-prey interaction, with the lemmings playing the role of predator and their food the prey: it is clear from the analysis presented here that a lemming-vegetation system containing realistic interaction elements can naturally give rise to stable limit-cycle behavior. Similarly, to regard the familiar and regular oscillations of the lynx and hare populations recorded by the

Hudson's Bay Trading Company (*24*) as resulting from a pure Lotka-Volterra oscillation about a neutrally stable equilibrium point, which is to say, having an amplitude determined by some environmental shock over 100 years ago, is quite implausible: this system, with the maximum hare population being constant to within a factor of 2 over 100 years or nine cycles, is surely the outcome of some stable limit cycle. This outcome, as we have just seen, can easily arise from the nonlinear food-hare-predators web.

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References and Notes

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17. The theorem also holds in general when any of the conditions given by Eqs. 3 and 4 are equalities rather than inequalities. This can be seen if one uses the methods indicated in (*16*). There can be special exceptions here, but none of the prey-predator forms catalogued in the text constitutes such an exception, as the equalities are attained as sensible limiting cases of more general predator-prey terms which obey the inequalities given in Eqs. 3 and 4. In particular, in the example given in Eq. 2 the theorem is rigorously obeyed, although here $\partial h/\partial y = 0$ rather than a negative quantity (that is, there is no predator intraspecific interaction).
18. The criterion given in Eq. 3 usually requires that the per capita prey birth rate be a monotonic decreasing function of increasing x. This condition is violated if there is an "Allee effect" [W. C. Allee, *The Social Life of Animals* (Heinemann, London, 1939)] whereby the per capita birth rate falls off at small x. This result makes sense biologically: models incorporating the effect should permit the possibility of extinction. However, Kolmogorov's theorem still applies in a restricted part of the x-y plane, thus allowing the possibility of limit cycles wherein the minimum in the prey population remains large enough for its Allee effect not to operate.
19. This estimate is obtained from Eq. 2 on the assumption that the rates r and b are comparable, that $x^*/K << 1$, and that cx^*, fx^* are less than, or of the order of, unity (x^* and y^* are the populations satisfying $dx/dt = dy/dt = 0$). One may then obtain rough piecewise continuous approximations for the limit cycle trajectory $x^\dagger(t)$, $y^\dagger(t)$ in the four regions where $x^\dagger(t)$ and $y^\dagger(t)$ are small or large as compared with the (unstable) equilibrium point values x^*, y^*. I have tested the usefulness of this estimation procedure, which leads to Eq. 10, by comparing it with a series of exact computer solutions for the limit cycle. The approximation given in Eq. 10 gave good order-of-magnitude agreement in every case tested.
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25. I thank the people at Magdalen College, Oxford, and at the Institute for Advanced Study, Princeton, for their hospitality during my leave from the University of Sydney, Australia. I also thank M. L. Rosenzweig for some constructive comments. Research sponsored by NSF grant GP-16147 A 1.

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Enriched Predator-Prey Systems: Theoretical Stability

Rosenzweig has warned that enrichment may destroy predator-prey systems (*1*). Using the graphical predation theory he and MacArthur developed (*2*), Rosenzweig has predicted that enrichment may cause previously persistent ecological systems to explode. This will happen, he says, when enrichment shifts the peak of the prey zero isocline (the collection of points in the phase plane at which the prey population does not change in density) to the right of the predator zero isocline. McAllister *et al.* (*3*) have challenged this prediction on experimental grounds. In this technical comment I shall show that Rosenzweig's own models do not fully support his conclusions, that the theory on which his arguments are based was incomplete and insufficient, and that there is therefore no inconsistency here between theory and experiment.

Rosenzweig studied what he believed to be six reasonable deterministic models of predator-prey interaction (*1*). He concluded that all show danger of extinction with increasing enrichment. He particularly concentrated on the following model [model 4 in (*1*)]:

$$dV/dt = rV(1 - V/K) - kP(1 - e^{-cV}) \qquad (1)$$

$$dP/dt = AkP(e^{-cJ} - e^{-cV}) \qquad (2)$$

where V is the prey (victim) density, P is the predator density, and K is the carrying capacity of the prey. The predator zero isocline is at $V = J$. The other parameters in Eqs. 1 and 2 influence the shape of the prey zero isocline and the rate of the system's response.

Investigating Eqs. 1 and 2, Rosenzweig first shows that the prey zero isocline conforms to the expectations of graphical predation theory; that is, it is peaked. He next shows that enrichment, increased K, moves this peak to a larger value of V and that it may therefore move it to the right of the predator zero isocline. According to graphical predation theory, he then predicts that this may cause the populations to go to extinction. Rosenzweig numerically integrates Eqs. 1 and 2 and finds that, for a large value of K, this does indeed happen.

I have used a digital computer to study the behavior of Eqs. 1 and 2. My results are not in complete accord with Rosenzweig's predictions. I find that the populations do not go to extinction when the peak of the prey zero isocline lies to the right of the predator zero isocline.

The numerical values of the parameters in Eqs. 1 and 2 are relatively unimportant, so I have chosen the following numbers so as to make my system quantitatively similar to the system Rosenzweig depicts in figure 1 of (*1*): $r = 0.05$; $k = 0.025$; $c = 0.1$; $A = 1$; and $J = 20$. For a single predator zero isocline, I determined the dynamic response for five different prey zero isoclines (Fig. 1A). Figure 1B shows a system for which the enrichment is too low: the predator population goes to extinction. Figure 1, C and D, shows stable systems that approach a steady state at the point where the two zero isoclines intersect. These results are in accord with graphical predation theory.

Figure 1, E and F, shows systems that, according to graphical predation theory, may go to extinction. Obviously, they do not. Both reach stable limit cycles. In fact, no matter how great K may be, the populations modeled by