
Nonlinear Systems and Applications

An International Conference

edited by

V. Lakshmikantham

*Department of Mathematics
University of Texas at Arlington
Arlington, Texas*



Academic Press, Inc.

NEW YORK SAN FRANCISCO LONDON 1977

A Subsidiary of Harcourt Brace Jovanovich, Publishers

TIME DELAYS IN PREDATOR-PREY SYSTEMS

J. M. Cushing
University of Arizona

The integrodifferential system

$$(1) \quad \begin{aligned} N_1' &= b_1 N_1 (1 - c_{11} N_1 - c_{12} \int_0^\infty N_2(t-u) k_1(u) du) \\ N_2' &= b_2 N_2 (-1 + c_{21} \int_0^\infty N_1(t-u) k_2(u) du) \\ c_{i,j} &> 0, \quad b_i > 0, \quad k_i(u) \geq 0, \quad \int_0^\infty k_i(u) du = 1 \end{aligned}$$

describes the dynamics of a predator-prey interaction where N_1 and N_2 measure (in some appropriate units) the population sizes of the prey and predator species respectively. Here the interaction terms represented by the integrals account for delay effects (over possibly all past times) which interactions with the opposite species have on the growth rate of each species. The coefficient c_{11} accounts for density effects within the prey population and $1/c_{11}$ is called the "carrying capacity" of the prey. The coefficients b_1 and b_2 are the natural birth and death rates of N_1 and N_2 respectively in the absence of all constraints.

Volterra first considered such delay systems in his well-known book [5]. Although not a great deal is known about the solutions of (1), some recent work has been concerned with its study as well as with more general systems (see [1-4]) and it is now possible to describe rather completely certain aspects of the qualitative behavior of solutions (as $t \rightarrow +\infty$) as they are functions of the parameters in the system.

The first simple observation we make is that all nonidentically zero solutions of (1) are obviously of one sign for all t . We will only be concerned with positive solutions here. We also observe that the only equilibria $(N_1, N_2) = (e_1, e_2) = \text{constant}$ lying in the right half plane are $E_1 : e_1 = 1/c_{21} > 0$,

$e_2 = (c_{21} - c_{11})/c_{12}c_{21}$ and $E_2 : e_1 = 1/c_{11}, e_2 = 0$. We describe the asymptotic behavior of solutions of (1) by means of four different cases which depend on the relative values of c_{ij} and b_i .

(i) First of all, in a manner very similar to a special case studied in [1], it can be proved that if $c_{11} > c_{21}$ then $(N_1(t), N_2(t)) \rightarrow (1/c_{11}, 0)$ as $t \rightarrow +\infty$ for all positive solutions of (1). In ecological terms, if the carrying capacity of the prey is less than the critical value $1/c_{21}$ then the predator goes extinct while the prey tends to this carrying capacity. (This can in fact be proved if $k_i(u)du$ is replaced by $dh_i(u)$ and hence is also true for systems with constant time lags.)

(ii) If c_{11} is less than, but close to c_{21} then the equilibrium E_1 is locally asymptotically stable. (Technically, given $\epsilon > 0$ there exists a $\delta > 0$ such that $|N_i(t)| < \delta$ for all $t < 0$ implies $|N_i(t)| < \epsilon$ for all $t \geq 0$ and a constant $\gamma > 0$ exists such that $|N_i(t)| < \gamma$ for all $t < 0$ implies $N_i(t) \rightarrow e_i$ as $t \rightarrow +\infty$.) This is proved by linearizing (1) about E_1 and by showing that the "eigenvalues" (i.e. the roots of the Paley-Weiner determinant [4]) of the resulting linear integrodifferential system have negative real parts provided c_{11} is close to, but less than c_{21} . This linearization procedure is formally justified for integrodifferential systems in [2]. Actually several numerically solved examples carried out by the author have all indicated that every positive solution tends to E_1 in this case and hence that the asymptotic stability of E_1 is in fact global in the first quadrant.

(iii) If $c_{11} > 0$ is small then the equilibrium E_1 is "usually" unstable. If again (1) is linearized about E_1 and if c_{11} is taken to be zero, then one finds that E_1 is unstable if the Paley-Wiener determinant, which turns out to be $f(s) = s^2 + K(s)$, has roots in the right half plane; here $K(s) = b_1 b_2 k_1^*(s) k_2^*(s)$ where $k_i^*(s)$ is the Laplace transform of $k_i(u)$. In this event some roots will also lie in the right half plane

for c_{11} small. Often $K(s)$ is a rational function and $f(s)$ can be investigated by means of the Routh-Hurwitz criteria. For a more general criterion it is also possible to show by means of the argument principle that if $f(s)$ has no purely imaginary roots then it is unstable if and only if $\arg f(+\infty i) \neq \pi$. Inasmuch as it is easy to show that this limit equals $(2n+1)\pi$ for some $n = 0, \pm 1, \pm 2, \dots$ we see that all but one of infinitely many cases lead to instability. (The remaining case $n = 0$ turns out to yield asymptotic stability as in (ii).) In all cases worked out by the author (for specific kernels such as $k(u) = (\alpha u + \beta) \exp(-\delta u)$) instability has always been found. See [1] and [2] for examples.

(iv) The loss of the stability of E_1 as c_{11} decreases suggests the possible existence of limit cycles. The existence of periodic solutions for general two species interactions with delays was studied by means of bifurcation theory in [3]. If the techniques in [3] are applied to (1) one obtains the following results.

Define

$$S_{ij}(n) = C_{ij} \int_0^{\infty} k_i(u) \sin 2n\pi p^{-1} u \, du, \quad C_{ij}(n) = C_{ij} \int_0^{\infty} k_i(u) \cos 2n\pi p^{-1} u \, du$$

$$\sum_1(n) = S_{12}C_{21} + S_{21}C_{12}, \quad \sum_2(n) = S_{12}S_{21} - C_{12}C_{21}.$$

Consider the hypotheses:

$$(H1) \quad \sum_1(n) > 0, \quad \sum_2(n) < 0 \quad \text{for some integer } n \geq 1 \quad \text{and period } p > 0$$

$$(H2) \quad C_{21}(n) \neq 0 \quad \text{for } n \text{ in (H1)}$$

$$(H3) \quad \text{Either } n \sum_1(m) \neq m \sum_1(n) \quad \text{or } n^2 \sum_1(n) \sum_2(m) \neq m^2 \sum_1(m) \sum_2(n) \\ \text{for all } m \neq n \quad (n \text{ as in (H1)}), \quad m \text{ an integer } \geq 1.$$

The condition (H1) for some n and p is necessary and the

conditions (H1)-(H3) are sufficient for the bifurcation of p -periodic solutions of (1) from the equilibrium E_1 as the birth and death rates b_1 and b_2 pass through the critical values

$$b_1^0 = -2\pi p^{-1} c_{21} \sum_1(n) / c_{11} \sum_2(n), \quad b_2^0 = 2\pi p^{-1} c_{11} / (c_{21} - c_{11}) \sum_1(n)$$

for all other constants fixed and $0 < c_{11} < c_{21}$.

This result also holds for the more general case of Stieltjes integrals $k_i(u)du = dh_i(u)$ in (1) and hence for systems with constant time lags [3].

All four cases above have been fully demonstrated numerically by the author for selected kernels. Similar cases were predicted by different means for a special case of (1) in [1], where other numerical results can be found and related to the cases above.

REFERENCES

- [1] J. M. Bownds, and J. M. Cushing, *On the behavior of solutions of predator-prey equations with hereditary terms*, *Math. Biosci.* 26(1975), 41-54.
- [2] J. M. Cushing, *An operator equation and bounded solutions of integrodifferential systems*, *SIAM J. Math. Anal.* 6(1975), No. 3, 433-445.
- [3] J. M. Cushing, *Periodic solutions of two species interaction models with lags*, *Math. Biosci.* 31(1976), 143-156.
- [4] R. K. Miller, *Asymptotic stability and perturbations for linear Volterra integrodifferential systems*, appearing in *Delay and Functional Differential Equations and their Applications*, K. Schmitt, editor, New York, Academic Press, 1972.
- [5] V. Volterra, *Lecons sur la Théorie Mathématique de la Lutte par la Vie*, Paris, Gauthier-Villars, 1931.