

## On the Behavior of Solutions of Predator-Prey Equations with Hereditary Terms

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### ABSTRACT

Some global properties of solutions of the classical integrodifferential systems, introduced by Volterra in his study of two species predator-prey populations, are studied. It is shown for large logistic loads that the predator goes to extinction and the prey tends to its carrying capacity. By use of a nonlinear approximation it is shown that for smaller logistic loads a "critical point" is asymptotically stable, while for sufficiently small logistic loads this point is unstable. These cases are demonstrated numerically for the original integrodifferential system using parameters which were computed on the basis of experimental data of *S. Utida* for bean-weevil vs. braconid-wasp interactions. Moreover, numerical solutions suggest further varied behavior of solutions of this system.

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### I. BASIC EQUATIONS; CRITICAL POINTS AND LONG-TIME AVERAGES

It is well known that the classical Lotka-Volterra differential equations for a two-species, predator-prey system without self-inhibitive growth rates, namely

$$\begin{aligned} N_1' &= N_1(a_1 - a_{12}N_2) && \text{(prey),} \\ N_2' &= N_2(-b_2 + b_{21}N_1) && \text{(predator),} \end{aligned} \tag{1}$$

with  $a_1, a_{12}, b_2, b_{21} > 0$ , have oscillatory, in fact periodic, solutions. This was shown by Volterra [1]; indeed, there exists a "constant of motion" which, when interpreted in other terms, amounts to the existence of a Lyapunov function for (1), the trajectory derivative of which is identically zero; see [2,

3] for this constant of motion. The proof of periodicity is dependent on this property.

The addition of "logistic" or inhibitive terms in (1) changes the system to

$$\begin{aligned} N_1' &= N_1(a_1 - a_{11}N_1 - a_{12}N_2), \\ N_2' &= N_2(-b_2 + b_{21}N_1 - b_{22}N_2), \end{aligned} \quad (2)$$

with  $a_{11}, b_{22} \geq 0$ , although it is evidently customary to assume in practice that the predator's inherent growth does not appreciably involve a logistic term and so  $b_{22} = 0$ ; see [4]. Regarding (2), Volterra showed that the solutions are still oscillatory about and tend to that system's stable equilibrium point. This is easily seen to be the case by observing that the so-called constant of motion for (1) again serves as a positive definite functional for (2) which has a negative trajectory derivative if  $a_{11} > 0$ ; without details here, this is used to show that the nontrivial equilibrium for (2) is asymptotically stable.

The verification of the basic model leading to (1) has been the subject of some experimental work over the years, with some investigators in agreement that a sort of oscillation is observable for predator-prey situations, although these oscillations can vary quite significantly from cycle to cycle. Early experiments by Gause [5] and Utida [6] tended to show that oscillations were quite difficult to see in a laboratory. Later work by both authors and others [7-10] tended to demonstrate definite, however loose, oscillatory behavior.

In this paper we describe some properties of solutions to a predator-prey system in which it is assumed that the rate of change of predators at time  $t$ ,  $N_2'(t)$ , depends on the exposure to prey over an *interval* of time  $[t-T, t]$  ( $T \geq 0$ ) rather than simply at the instant  $t$ . With this change, the system may be written as

$$N_1' = N_1(a_1 - a_{11}N_1 - a_{12}N_2) \quad (3a)$$

$$N_2' = N_2\left(-b_2 + \int_0^t k(t-s)N_1(s)ds - b_{22}N_2\right), \quad (3b)$$

where  $k$  is a non-negative, continuous function and  $k(t) \equiv 0$  for  $t > T$ . This is basically the same system originally considered by Volterra [1] except there the integral has the form

$$\int_{-\infty}^t \quad \text{instead of} \quad \int_0^t.$$

Also, similarly to that original work, the assumption that  $k(t)$  vanishes after

$t = T$  amounts to an assumption that the cumulative contribution in the term

$$\int_0^t k(t-s)N_1(s) ds$$

is effectively realized only on the interval  $[t-T, t]$  if  $t \geq T$ . This is clear from the computation:

$$\int_0^t k(t-s)N_1(s) ds = \int_0^T k(s)N_1(t-s) ds = \int_{t-T}^t k(t-s)N_1(s) ds, \quad t \geq T.$$

The two derivations of the model are equivalent except that the original work assumed knowledge of the function  $N_1$  on  $(-\infty, t)$ ; the system in (3) requires no such knowledge and, furthermore, is classically well posed with the addition of initial values.

The main goal here is to describe some of the features of solutions of (3). In Sec. II certain qualitative aspects of solutions to (3) are deduced assuming a truncated Taylor series approximation for  $N_1$ . This particular approximation has been used by Cunningham [11] in an investigation of predator-prey systems with a single time lag. As shown below, certain results of this approximation are verified numerically, a situation which lends additional credence to its qualitative accuracy as applied to (3). Numerical calculations have been used previously to show the behavior of solutions to the Volterra integrodifferential equations [2]. That work, however, assumed constant (therefore non-integrable) kernels, an assumption which not only eliminates certain analytical techniques but is possibly unrealistic when compared with Volterra's original derivation in [1].

Initially, we observe that the system (3) has no nontrivial equilibrium point. Nevertheless, it is interesting and fruitful to consider what might still be referred to as a critical point  $(P_1, P_2)$  given by the equations

$$\begin{aligned} a_{11}P_1 + a_{12}P_2 &= a_1 \\ k^*P_1 - b_{22}P_2 &= b_2, \end{aligned} \quad (4)$$

where  $k^* = \int_0^\infty k(t) dt = \int_0^T k(t) dt$ . It is not difficult to see that if  $(N_1(t), N_2(t))$  has a limit as  $t \rightarrow +\infty$ , then it must be  $(P_1, P_2)$ . However, it can also be shown that there exist quite reasonable kernels of the above type such that this critical point is always unstable in the usual (Lyapunov) sense<sup>1</sup> (if there are no logistic terms,  $a_{11} = b_{22} = 0$ ), and a numerical example below indicates that  $(P_1, P_2)$  can be unstable even though  $(N_1(t), N_2(t))$  apparently tends to  $(P_1, P_2)$  as  $t \rightarrow +\infty$ . From the point of view of modeling with practical application in mind, this possibly indicates that the strict

mathematical concept of stability may not be useful in determining what could reasonably be called "practical" stability by a population biologist.

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<sup>1</sup>We would say that the (nonsolution) point  $(P_1, P_2)$  is *stable* if given  $\epsilon > 0$  there exists a  $\delta > 0$  such that  $d[(N_1(0), N_2(0)), (P_1, P_2)] < \delta$  implies  $d[(N_1(t), N_2(t)), (P_1, P_2)] < \epsilon$  for all  $t > 0$ . Here  $d[ \ , \ ]$  denotes some vector metric.

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As will be seen below, if  $(P_1, P_2)$  is in the first quadrant, it is apparently possible for solutions to (3) to revolve about  $(P_1, P_2)$  in any of three distinct ways: spiraling in, spiraling out, or simply oscillating in some approximately periodic manner. In any case, as the theorem immediately to follow shows, the point  $(P_1, P_2)$  is the long-time average of  $(N_1(t), N_2(t))$  provided both  $N_1(t)$  and  $N_2(t)$  are bounded away from zero and are bounded above. It is, incidentally, not difficult to show that  $N_1(t)$  is always bounded above and neither  $N_1(t)$  nor  $N_2(t)$  can vanish in a finite length of time. This theorem strongly resembles one of Volterra [1]; it also generalizes a result for the basic equations (1).

**THEOREM 1**

*If there exist  $m, M$  such that  $0 < m \leq N_1(t), N_2(t) \leq M < \infty$  for all  $t \geq 0$  and if  $k$  is continuous and integrable on  $[0, \infty]$ , then  $P_1 > 0, P_2 > 0$  and*

$$[N_i] = \lim_{t \rightarrow +\infty} t^{-1} \int_0^t N_i(t) dt = P_i, \quad i = 1, 2,$$

where  $P_1, P_2$  are given by (4).

*Proof.* From the equations (3) we have

$$t^{-1} \ln \left( \frac{N_1(t)}{N_1(0)} \right) = t^{-1} \int_0^t [a_1 - a_{11}N_1(s) - a_{12}N_2(s)] ds,$$

and

$$t^{-1} \ln \left( \frac{N_2(t)}{N_2(0)} \right) = t^{-1} \int_0^t \left( -b_2 + \int_0^s k(s-u)N_1(u) du - b_{22}N_2(s) \right) ds.$$

With the current assumptions, this implies that

$$0 = a_1 - a_{11}[N_1] - a_{12}[N_2]$$

and

$$0 = -b_2 + \lim t^{-1} \int_0^t \int_0^s k(s-u)N_1(u)du ds - b_{22}[N_2], \quad t \rightarrow +\infty.$$

It will be true that  $[N_1], [N_2]$  satisfy the same equations as those satisfied by  $P_1$  and  $P_2$  (and hence  $[N_k] = P_i$ ) if we show that

$$\lim t^{-1} \int_0^t \int_0^s k(s-u)N_1(u)du ds = k^*[N_1].$$

This is true, however, because

$$\begin{aligned} & \left| t^{-1} \int_0^t \int_0^s k(s-u)N_1(u)du ds - k^*[N_1] \right| \\ &= \left| t^{-1} \int_0^t \left( \int_0^t k(s-u)N_1(u)du - k^*N_1(s) \right) ds \right| \\ &= \left| t^{-1} \int_0^t \left( \int_u^t k(s-u)ds N_1(u) - k^*N_1(u) \right) du \right| \\ &= t^{-1} \int_0^t \left( k^* - \int_u^t k(s-u)ds \right) |N_1(u)| du \\ &\leq Mt^{-1} \int_0^t \left( k^* - \int_u^t k(s-u)ds \right) du. \end{aligned}$$

Now, if the last integral is a bounded function of  $t$ , then

$$t^{-1} \int_0^t \left( k^* - \int_u^t k(s-u)ds \right) du \rightarrow 0 \quad \text{as } t \rightarrow +\infty,$$

and the theorem is proved. If this integral is not bounded, then

$$\int_0^t \left( k^* - \int_u^t k(s-u)ds \right) du \rightarrow +\infty \quad \text{as } t \rightarrow +\infty,$$

and (by l'Hospital's Theorem):

$$\lim t^{-1} \int_0^t \left( k^* - \int_u^t k(s-u)ds \right) du = \lim \left( k^* - \int_0^t k(t-u)du \right) = 0$$

and the theorem is proved.

II. AN APPROXIMATION;  
PHASE-PLANE ANALYSIS FOR (3)

Our purpose in this section is to illustrate some of the variety in qualitative behavior exhibited by solutions of the system (3). First, we show that if  $k^*a_1 > b_2a_{11}$ , then all solutions  $(N_1, N_2)$  of (3) tend to  $(a_1/a_{11}, 0)$ . Secondly, we consider the more difficult case  $k^*a_1 < b_2a_{11}$ ; this we do by replacing (3) by a certain nonlinear (differential) approximation. Straight-forward analysis of this approximation shows the possibility of stability or instability depending upon the relationship among the parameters in (3); this approach was previously taken in [11] for the purpose of studying a system with discrete time lags. The important special case  $b_{22}=0$  is considered in more detail; the conclusions for this case will be corroborated by the numerical results in Sec. III.

We assume throughout that the hereditary kernel  $k$  is as above; that is, there exists a  $T < +\infty$  such that  $k(t)=0$  for  $t \geq T$ .

LEMMA 1

Let  $k^* = \int_0^{+\infty} k(s) ds < +\infty$  and suppose  $N(t) \rightarrow N(\infty)$  as  $t \rightarrow +\infty$ . Then  $\int_0^t k(t-s)N(s) ds \rightarrow k^*N(\infty)$  as  $t \rightarrow \infty$ .

*Proof.* Notice that for  $t \geq T$

$$k^*N(\infty) = \int_0^\infty k(s)N(\infty) ds = \int_0^T k(s)N(\infty) ds.$$

Then since

$$\int_0^t k(t-s)N(s) ds = \int_0^T k(s)N(t-s) ds \quad \text{for } t \geq T,$$

we have for  $t \geq T$

$$\left| \int_0^t k(t-s)N(s) ds - k^*N(\infty) \right| \leq \int_0^T |k(s)| |N(t-s) - N(\infty)| ds.$$

Letting  $t \rightarrow +\infty$  and using the dominated convergence theorem we obtain the desired result.

LEMMA 2

Let  $N_1(t) \geq 0$ ,  $N_2(t) \geq 0$ , solve (3) for  $t \geq 0$ . Then either (a)  $N_1(t)$  decreases monotonically to  $a_1/a_{11}$  as  $t \rightarrow \infty$  or (b) there exists a  $t' > 0$  such that  $N_1(t) \leq a_1/a_{11}$  for all  $t \geq t'$ .

*Proof.*

(i) Suppose  $N_1(0) > a_1/a_{11}$ . Then for as long as  $N_1(t) > a_1/a_{11}$ , we see from (3a) that  $N_1' < 0$ . Thus, either  $N_1$  decreases monotonically for all  $t \geq 0$  or  $N_1(t) = a_1/a_{11}$  for some first  $t' > 0$ .

Consider the first possibility. In this case  $N_1(\infty)$  exists and  $N_1(\infty) \geq a_1/a_{11}$ ; we wish to rule out inequality. If  $N_1(\infty) > a_1/a_{11}$ , then  $N_1(t) > N_1(\infty) > a_1/a_{11}$  for all  $t \geq 0$ , which implies from (3a) that  $N_1' \leq N_1[a_1 - a_{11}N_1(\infty)]$  and hence  $N_1$  tends exponentially to zero, a contradiction.

In the second case we wish to show that in fact  $N_1(t) \leq a_1/a_{11}$  for all  $t \geq t'$ . If  $N_1(t'') > a_1/a_{11}$  for some  $t'' > t'$ , then there would exist  $t''' \in (t', t'')$  for which  $N_1(t''') > a_1/a_{11}$  and  $N_1'(t''') > 0$ , which contradicts (3a). This proves the lemma for  $N_1(0) > a_1/a_{11}$ .

(ii) Suppose  $N_1(0) \leq a_1/a_{11}$ . Then  $N_1(t) \leq a_1/a_{11}$  for all  $t \geq 0$ . This follows exactly as in the end of the proof of part (i) above.

a.  $k^*a_1 < b_2a_{11}$

The main result of this subsection is that the predator  $N_2$  becomes extinct and the prey  $N_1$  tends to its carrying capacity.

**THEOREM 2**

*If  $k^*a_1 < b_2a_{11}$ , then all solutions  $N_1 > 0$ ,  $N_2 > 0$  of (3) satisfy  $N_1 \rightarrow a_1/a_{11}$ ,  $N_2 \rightarrow 0$  as  $t \rightarrow +\infty$ .*

*Proof.* There are, according to Lemma 2, two possibilities for  $N_1$ . Using Lemma 1 we find for these two cases respectively

$$\lim_{t \rightarrow \infty} \left( -b_2 + \int_0^t k(t-s)N_1(s) ds \right) = -b_2 + k^*a_1/a_{11} < 0$$

or

$$-b_2 + \int_0^t k(t-s)N_1(s) ds \leq -b_2 + k^*a_1/a_{11} < 0, \quad t \geq t' + T.$$

Thus, in either case, we have from (3b) that  $N_2' \leq \frac{1}{2}N_2(-b_2 + k^*a_1/a_{11})$  for all large  $t$ , which in turn implies  $N_2 \rightarrow 0$ .

Finally we must argue that  $N_1 \rightarrow a_1/a_{11}$ . First, suppose  $N_1$  has no limit as  $t \rightarrow \infty$ . Let  $l = \liminf_{t \rightarrow \infty} N_1(t) \geq 0$ ; by Lemma 2,  $l < a_1/a_{11}$ . Let  $t_n > 0$  be chosen so that  $t_n \rightarrow \infty$  as  $n \rightarrow \infty$ ,  $N(t_n) \rightarrow l$ , and  $N'(t_n) = 0$ . Then for all  $n$

$$0 = N'(t_n) = N_1(t_n)[a_1 - a_{11}N_1(t_n) - a_{12}N_2(t_n)]$$

or

$$0 = a_1 - a_{11}N_1(t_n) - a_{12}N_2(t_n).$$

Letting  $n \rightarrow \infty$ , we obtain the contradiction  $l = a_1/a_{11}$ , and conclude  $N_1$  has a limit  $N_1(\infty)$  as  $t \rightarrow \infty$ . To finish the proof we must show  $N_1(\infty) = a_1/a_{11}$ .

By Lemma 2,  $N_1(\infty) \leq a_1/a_{11}$ . Suppose  $N_1(\infty) < a_1/a_{11}$ . Then there exists a number  $\delta > 0$  and a  $t' > 0$  such that  $N_1(t) \leq -2\delta + a_1/a_{11}$  for all  $t \geq t'$ . Since  $N_2 \rightarrow 0$  as  $t \rightarrow \infty$ , we may assume  $t'$  is so large that  $N_2 \leq \delta a_{11}/a_{12}$  for  $t \geq t'$ . Then from (3a) we conclude that  $N_1' \geq \delta a_{11} N_1$  and hence  $N_1 \rightarrow +\infty$ . This contradicts Lemma 2 and proves  $N_1(\infty) = a_1/a_{11}$ .

b.  $k^* a_1 > b_2 a_{11}$

We investigate this case by replacing (3) with an approximation obtained by substituting the truncated Taylor series  $N_1(t) - sN_1'(t)$  for  $N_1(t-s)$  in the integral term

$$\int_0^t k(t-s)N_1(s)ds = \int_0^t k(s)N_1(t-s)ds,$$

which then becomes, for  $t \geq T$ ,

$$\begin{aligned} N_1 \int_0^t k(s)ds - N_1' \int_0^t sk(s)ds &= N_1 k^* - N_1' m \\ &= N_1 k^* - m N_1 (a_1 - a_{11} N_1 - a_{12} N_2), \end{aligned}$$

where  $m = \int_0^T sk(s)ds$  is the first moment of  $k$ . Thus, the system (3) becomes, for  $t \geq T$ ,

$$N_1' = N_1 (a_1 - a_{11} N_1 - a_{12} N_2), \quad (3'a)$$

$$N_2' = N_2 [-b_2 + (k^* - ma_1)N_1 - b_{22}N_2 + ma_{11}N_1^2 + ma_{12}N_1N_2]. \quad (3'b)$$

It is not difficult to draw a direction field in the first quadrant for this system of nonlinear differential equations. This is done in Fig. 1, where  $L$  denotes the straight line  $a_1 - a_{11}N_1 - a_{12}N_2 = 0$ ,  $Q$  denotes the hyperbola

$$-b_2 + (k^* - ma_1)N_1 - b_{22}N_2 + ma_{11}N_1^2 + ma_{12}N_1N_2 = 0,$$

and  $P = (P_1, P_2)$  denotes their unique intersection point

$$P_1 = \frac{a_{12}b_2 + a_1b_{22}}{a_{12}k^* + a_{11}b_{22}}, \quad P_2 = \frac{a_1k^* - a_{11}b_2}{a_{12}k^* + a_{11}b_{22}},$$

which lies in the first quadrant because of the assumption  $k^* a_1 > b_2 a_{11}$ . This direction field falls into three cases depending on the hyperbola  $Q$  and its relation to  $L$ ; however, in all cases, the field spirals counterclockwise around the critical point  $P$ .

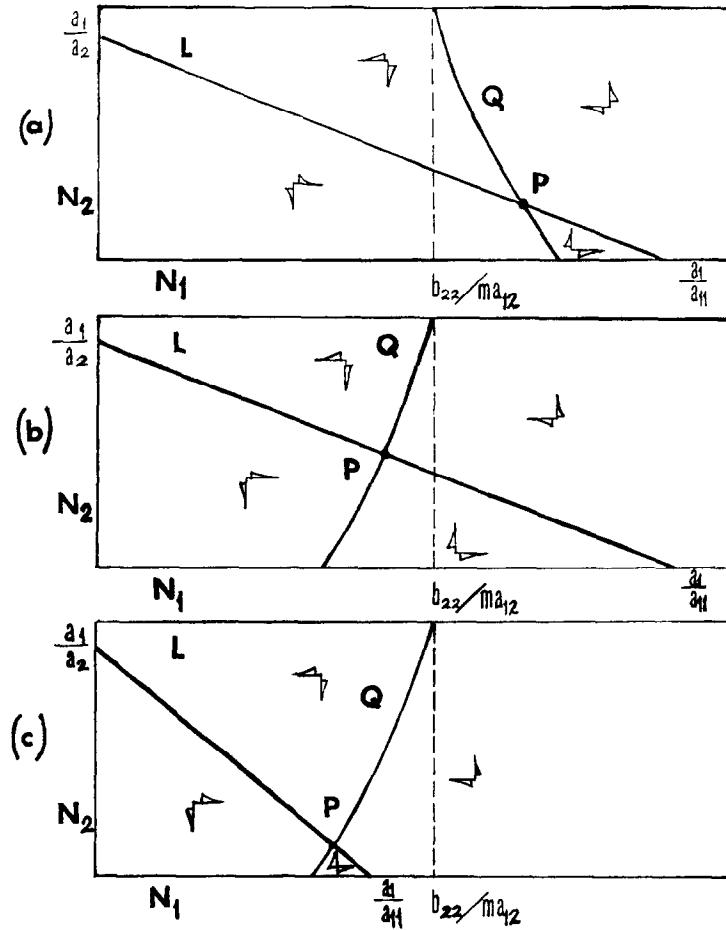


FIG. 1. Phase-plane analysis for the approximate system (3').

To investigate the nature of the spiral trajectory, at least locally near  $P=(P_1, P_2)$ , we linearize the system (3') at the point  $P$ . Standard theorems [13] insure that the local behavior of (3') is that of this linearization. The resulting linearized system

$$N_1' = -a_{11}P_1N_1 - a_{12}P_1N_2,$$

$$N_2' = P_2(k^* + ma_{11}P_1)N_1 + P_2(ma_{12}P_1 - b_{22})N_2$$

has eigenvalues  $\frac{1}{2}[A \pm (A^2 - B)^{1/2}]$  where  $B = P_1 P_2 (a_{12} k^* + a_{11} b_{22}) > 0$  and

$$A = P_2 (m a_{12} P_1 - b_{22}) - a_{11} P_1. \quad (4)$$

It is not difficult to see that the sign of the real parts of these eigenvalues is that of  $A$ , and consequently the local behavior (3') near  $P$  is spirally stable if  $A < 0$ . Furthermore, arguing as in the proof of Lemma 2 [for (3') instead of (3)], one can show that, for all solutions of (3'),  $N_1$  is ultimately bounded by  $a_1/a_{11}$ . From this fact and the fact that  $N_2$  cannot tend to  $\infty$  as  $t \rightarrow \infty$  [for then, by (3'a),  $N_1 \rightarrow 0$  as  $t \rightarrow \infty$  and from (3'b),  $N_2 \rightarrow 0$  as  $t \rightarrow \infty$ , a contradiction], we can see from the direction field drawn in Fig. 1 that in the event of spiral instability ( $A > 0$ ) system (3') has, by the Poincaré-Bendixson Theorem, at least one periodic, nonconstant limit cycle.

### THEOREM 3

*The direction field for the nonlinear approximation (3') to the hereditary system (3) is counterclockwise spiral around the critical point*

$$P_1 = \frac{a_{12} b_2 + a_1 b_{22}}{a_{12} k^* + a_{11} b_{22}}, \quad P_2 = \frac{a_1 k^* - a_{11} b_2}{a_{12} k^* + a_{11} b_{22}}.$$

*All solutions are bounded, and the critical point is locally stable if  $A < 0$  and unstable if  $A > 0$  [ $A$  given by (4)], where in the latter case a nonconstant periodic limit cycle exists.*

Although we make no rigorous attempt to prove that the original system (3) has the properties of the approximation (3') described in the above theorem, we point out that numerical results presented below indicate that (3) possesses the same properties described in this theorem.

#### c. $b_{22} = 0$

In concluding this section, we briefly consider the important case when  $b_{22} = 0$ , which is considered numerically below. In this case the stable and unstable cases discussed in the theorem are distinguished by the sign of  $A = P_1 (m a_{12} P_2 - a_{11})$  or, since  $P_1 > 0$ , by the sign of

$$m a_{12} P_2 - a_{11} = \frac{m a_1 a_{12} k^* - a_{11} (m a_{12} b_2 + a_{12} k^*)}{a_{12} k^*}.$$

Thus, treating the logistic load  $a_{11}$  as a free parameter and the remaining parameters as fixed, we find that the approximate system (3') is locally stable or unstable according as  $a_{11}$  is greater than or less than  $c = (m a_1 a_{12} k^*) / (m a_{12} b_2 + a_{12} k^*)$ . Noting that  $c < k^* a_1 / b_2$ , we may summarize the situation for the case  $b_{22} = 0$  as follows:

- (1)  $a_{11} > k^* a_1 / b_2$  implies global asymptotic stability of the point  $P = (a_1 / a_{11}, 0)$ ;  
 (2)  $c < a_{11} < k^* a_1 / b_2$  implies local spiral stability of the point  $P = (P_1, P_2)$ ;  
 (3)  $0 \leq a_{11} \leq c$  implies local spiral instability of the point  $P$ .

Numerical results for the original integrodifferential system (3) seem to indicate that cases (2) and (3) are in fact global. The actual quantity  $c$ , which separates these cases, does not appear to be particularly accurate when compared to the numerically computed value which separates outward and inward spirals in the example below.

### III. NUMERICAL EXAMPLES; A SPECIFIC KERNEL

Here we consider specific examples of systems of the form (3). The specific coefficients used were computed using a least-squares technique applied to certain generations in bean weevil v. braconid wasp found in the work of S. Utida [8]. The point of consideration here is to corroborate numerically some of the qualitative features of the approximation in Sec. III, and on the other hand, to show behavior which contrasts with that experienced in the usual phase-plane analysis for autonomous differential equations.

For the current purposes, the kernel  $k$  in (3) must be explicit. In view of Volterra's derivation,

$$k(t-s) = \gamma \psi(t-s) f(t-s),$$

where, according to the "law of encounters" (Volterra [1, p. 144]),  $\psi(t-s)$   $N_1(s)$  represents the expected number of predators of offspring born in the interval  $[s, s + ds]$  per female parent of age at least  $t-s$ , and  $f(t-s)N_2(t)$  represents the number of (female) predators of age greater than  $t-s$  alive at time  $t$ . Hence, to assume that  $k(t)$  is zero for all  $t \geq T$  ( $T < +\infty$ ) is to assume that we expect no progeny from female predators of age at least  $T$ . In the absence of more specific information on what the qualitative features of  $k$  should be, we assume that a reasonable choice might be

$$k(t) = \begin{cases} (\alpha + \beta t)e^{-\delta t}, & 0 \leq t < T, \\ 0, & t \geq T, \end{cases}$$

where  $\alpha$ ,  $\beta$ ,  $\delta$  and  $T$  are parameters which we attempt to adjust to data.

With the above assumption for  $k$ , a specific application of a least-squares determination of  $a_1$ ,  $a_{12}$ ,  $a_{11}$ ,  $b_2$ ,  $b_{22}$ ,  $\alpha$  and  $\beta$  from bean-weevil v.

braconid-wasp data in [8] (population  $E$ , generations 1 to 38) yields

$$\begin{aligned} N_1' &= N_1(6.21 \times 10^{-1} - a_{11}N_1 - 2.04 \times 10^{-3}N_2), \\ N_2' &= N_2\left(-3.17 \times 10^{-1} + \int_0^t k(t-s)N_1(s)ds\right), \end{aligned} \quad (5)$$

where

$$k(t-s) = \begin{cases} [3.52 \times 10^{-4} + 1.45 \times 10^{-1}(t-s)]e^{-10(t-s)}, & 0 \leq t-s < 1, \\ 0, & t-s \geq 1. \end{cases}$$

(The actual computations imply  $a_{11} = 0$ ; however, for the present purposes we consider this coefficient as a parameter.) The choice  $T = 1$  generation seemed reasonable;  $\delta = 10$  is an arbitrary choice. This system was integrated using an improved Euler method of the type described by Noble [14]. No attempt to obtain great accuracy was made, inasmuch as the main goal was to produce comparative qualitative information on solution curves. The general shapes of computed solution curves are depicted below. Figure 2(a-c) demonstrates the three cases (1), (2) and (3) described at the end of

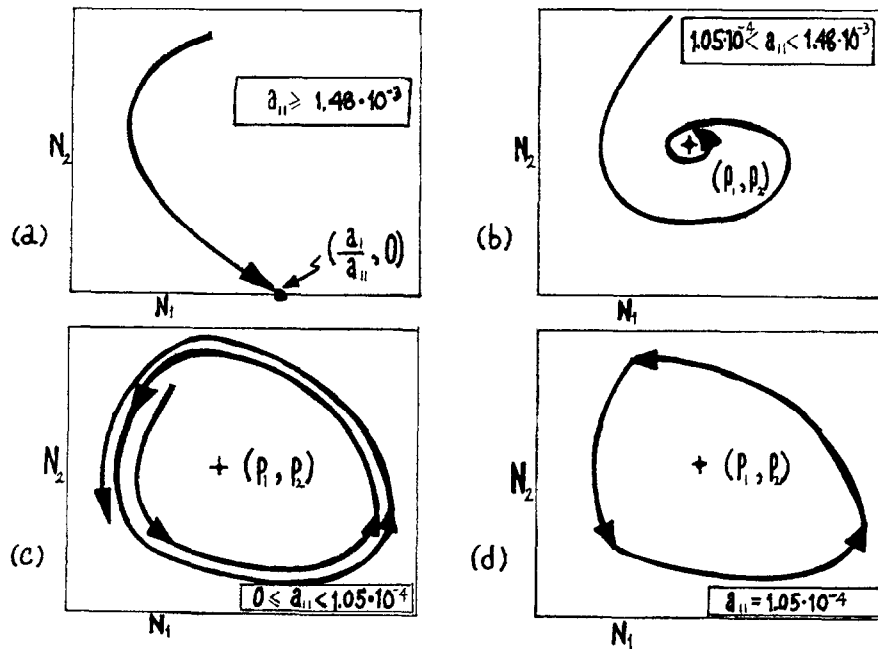


FIG. 2. Qualitative nature of numerical solutions to Eq. (5) for various logistic loads  $a_{11}$ :  $N_1$  is the prey (bean weevil);  $N_2$  is the predator (wasp);  $(P_1, P_2)$  is the "critical point".

the last section. Figure 2(d) represents the boundary between cases (2) and (3), and although the solution  $(N_1(t), N_2(t))$  is not periodic, it is apparently asymptotically periodic in some sense. Figure 3 demonstrates the case where a solution curve crosses itself, a situation which does not happen with differential models; this particular example also suggests that the “critical point”  $(P_1, P_2)$  is unstable, although  $(N_1(t), N_2(t))$  evidently tends to  $(P_1, P_2)$  as  $t$  gets large.

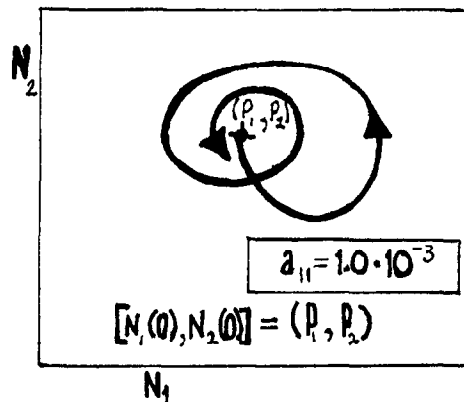


FIG. 3. Qualitative nature of numerical solutions to Eq. (5) for various logistic loads  $a_{11}$ :  $N_1$  is the prey (bean weevil);  $N_2$  is the predator (wasp);  $(P_1, P_2)$  is the “critical point”.

We observe that for our particular choice of  $k$ , there is a trade-off in basic behavior between the inclusion of an integral term and a logistic term  $a_{11}$ : the integral tends to cause outward spirals, while the logistic tends to cause inward spirals.

In summary, we note that most of the experimental data [7–10] which were intended to corroborate theoretical predator-prey models have been compared with the system (1). Utida [8] has suggested that logistics [see (2)] play a major role describing his data. Here we have seen that a reconsideration of a “hereditary” model (3) may play an important role in model verification of data, simply due to the additionally varied behavior of solutions which do not occur in the basic models (1) and (2). On the other hand, as shown in Sec. II and verified in Sec. III, certain aspects of solutions to (3) can be studied and predicted by converting (3) to an autonomous differential equation via a certain approximation and performing the usual phase-plane analysis.

*Note added in proof.* In the proof of Theorem 1, the limits  $[N_1]$  and  $[N_2]$  are assumed to exist. This is easily proved, however, by repeating the supplied argument respectively with  $\limsup$  and  $\liminf$ , thus showing that both the  $\liminf$  and  $\limsup$  equal  $P_i$ .

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