STABILITY AND INSTABILITY IN PREDATOR-PREY MODELS WITH GROWTH RATE RESPONSE DELAYS

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We consider a general model for predator-prey interactions in which the instantaneous per unit growth rate $f_i = f_i(N_1, N_2)(t)$ of each species at any time t is a functional of species densities $N_i(s)$ at previous times $s \leq t$. We assume that the equation for prey density N_1 obtained from the model in the absence of predators ($N_2 = 0$) possesses at least one positive equilibrium $c > 0$ (which may or may not be stable). Our goal is to study the stability properties of positive equilibria $N_i = e_i > 0$ of the predator-prey system as they are functions of c.

Suppose the prey's growth rate response functional has the property that there exists at least one positive prey equilibrium c when $N_2 = 0$ (i.e., $f_1 = 0$ for $N_1 = c$, $N_2 = 0$) and that this parameter c is made explicit in the functionals f_i. Thus, we consider f_i to be a function of c as well as of $N_i(s)$, $s \leq t$. Specifically we assume

(H1)
$$\begin{cases} f_i : R_+^3 \to R, \ R_+ = \{\text{nonnegative reals}\}; \\ f_1(c, 0; c) = 0 \text{ for all } c \geq c_0 \text{ for some } c_0 \geq 0; \\ f_i(e_1, e_2; c) = 0 \text{ has a (not necessarily unique) solution} \\ e_i = e_i(c) \text{ which is continuous for } c \geq c_0, \ e_i(c) > 0 \text{ for} \\ c > c_0, \text{ and satisfies } 0 < e_i(+\infty) < +\infty, \ e_2(c_0) = 0; \end{cases}$$

and also

(H2)
$$\begin{cases} f_i(x_1, x_2; c) \text{ is twice continuously differentiable in } x_1 \text{ and } x_2 \\ \text{near } x_i = e_i(c) \text{ for every } c > c_0 \text{ and} \\ \quad a_{11}(c) > 0, \ a_{12}(c) > 0, \ a_{21}(c) > 0, \ a_{22}(c) = 0 \\ \quad a_{12}(+\infty) < +\infty, \ a_{21}(+\infty) < +\infty, \ a_{11}(+\infty) = 0 \\ \text{where } a_{ij}(c) := (-1)^i \partial f_i(e_1(c), e_2(c); c)/\partial x_j. \end{cases}$$

Finally, we assume

(H3)
$$e_2{}'(c_0) := \frac{d}{dc} e_2(c_0) > 0, \ e_1(c_0) = c_0.$$

Hypothesis (H1) guarantees that the prey has an equilibrium c of at least some minimal size c_0 and that for $c > c_0$ the predator-prey interaction has a positive equilibrium which approaches a finite point as c increases. Hypothesis (H1) also assumes (viz. $e_2(c_0) = 0$) that c_0 is the

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smallest value of c for which the branch of predator-prey equilibria $e_i(c)$ stays in the first quadrant (i.e., the infimum of those prey carrying capacities which could possibly support predation). The smoothness assumptions on f_i in (H2) allow us to linearize at the equilibrium $e_i(c)$ while the sign conditions in (H2) guarantee that the interaction near equilibrium is that of a predator and prey, that the first order interaction coefficients approach finite limits as c increases and finally that, to first order at equilibrium, only the prey density affects the predator's growth rate $(a_{22}(c) = 0)$. Lastly, (H3) demands that the equilibrium $e_i(c)$ crosses into the fourth quadrant transversally at $c = c_0$ and that the two branches of equilibria $(e_1(c), e_2(c))$ and $(c, 0)$ meet at $c = c_0$.

All of these hypotheses are, for example, met by the classical, linear response functionals

$$f_1(x_1, x_2; c) = b_1(1 - x_1/c - c_{12}x_2)$$

(1) $$f_2(x_1, x_2; c) = b_2(-1 + c_{21}x_1)$$

$$b_i > 0, \ c_{ij} > 0, \ c > 0$$

where $e_1 = 1/c_{21}$, $e_2 = (c - c_{21}^{-1})/cc_{12}$ and where $a_{ij} = b_i c_{ij}$ is independent of c for $i \neq j$, $a_{11} = b_1/c$ and $a_{22} = 0$. Here $c_0 = 1/c_{21} > 0$. This prototype model is in fact the basis on which the results of this paper are founded. The hypotheses are also met when the interspecific interaction terms in (1) are replaced by Holling response functionals $x_i/(1 + x_i)$, provided $c_{ij} > 1$, $i \neq j$.

Under the hypotheses above we consider the delay predator-prey model

$$N_i' = N_i f_i \left(\int_{-\infty}^{t} N_1(s)k_{i1}(t - s) \, ds, \right.$$

(S)

$$\left. \int_{-\infty}^{t} N_2(s)k_{i2}(t - s) \, ds; \, c \right), \, i = 1, 2$$

where the delay kernels k_{ij} satisfy

(H4) $\begin{cases} k_{ij}(s) \geq 0 \text{ are piece-wise continuous for } s \geq 0 \text{ with} \\ \int_0^\infty k_{ij}(s) \, ds = 1 \text{ and } \int_0^\infty s k_{ij}(s) \, ds < +\infty. \end{cases}$

Under the stated hypotheses (S) has equilibria $N_1 = c$, $N_2 = 0$ and $N_1 = e_1(c) > 0$, $N_2 = e_2(c) > 0$ for all c. If, for a fixed $c > c_0$, (S) is linearized at the positive equilibrium $N_i = e_i(c)$ [3, 5] then a linear integrodifferential system

$$n_1' = -e_1 a_{11} \int_0^t n_1(s) k_{11}(t - s) \, ds$$

(L)
$$-e_1 a_{12} \int_0^t n_2(s) k_{12}(t - s) \, ds$$

$$n_2' = e_2 a_{21} \int_0^t n_1(s) k_{21}(t - s) \, ds$$

is obtained where $n_i = N_i - e_i$. The local stability of the equilibrium is determined by the location of the roots of the characteristic function of (L) given by

$$p(z, c) := z(z + e_1 a_{11} k_{11}^*(z))$$
$$+ e_1 e_2 a_{12} a_{21} k_{12}^*(z) k_{21}^*(z)$$

in the complex z-plane [5]. Here $k_{ij}^*(z)$ is the Laplace transform of $k_{ij}(t)$. If all roots lie in the left half plane (i.e., $p \neq 0$ for $\mathrm{Re}\, z \geqq 0$) then the equilibrium is (locally) asymptotically stable. If at least one root lies in the right half plane $\mathrm{Re}\, z > 0$ then the equilibrium is unstable. Our goal thus reduces to the study of p as a function of $c > c_0$.

In order to study p for large c we must first mention some results concerning the formal case when $c = +\infty$ (unlimited inherent prey resources) which may be found in [2, 3]. These results say roughly speaking that in this case the positive equilibrium is "usually" unstable.

LEMMA. *Under the hypothesis* (H4) *on* k_{12} *and* k_{21} *and the added condition that for* $\alpha > 0$ *the function*

$$p_\infty(z) := z^2 + \alpha k_{12}^*(z) k_{21}^*(z) \neq 0 \text{ for } \mathrm{Re}\, z = 0$$

we have that $\arg p_\infty(+i\infty) = (1 - 2m)\pi$ *for some integer* $m \geqq 0$ *and further that* $p_\infty(z) \neq 0$ *for* $\mathrm{Re}\, z \geqq 0$ *if and only if* $m = 0$. *Thus* $p_\infty(z) = 0$ *has at least one root with* $\mathrm{Re}\, z > 0$ *when* $m \geqq 1$ (*in fact* $2m$ *such roots*).

This lemma is Theorem 4 in [3, p. 43] and a proof can be found there (as well as in [2]). It implies that the positive equilibrium in the case of no prey self-inhibition (at least near equilibrium, i.e., $a_{11} = 0$) is usually unstable. This is because in only one case $m = 0$ of infinitely many cases is the equilibrium stable, because $m \neq 0$ for "generic" delay kernels which are of the form $T^{-1} \exp(-t/T)$ or $T^{-2} t \exp(-t/T)$ [3] and because even very "weak" delays cause instability as is shown by the following corollary.

COROLLARY. *Assume that* k_{12} *and* k_{21} *satisfy* (H4) *and that* $k''_{ij}(t) \geqq 0$, $k'_{ij}(t) \leqq 0$ *for all* $t > 0$ *and* $k_{ij}(+\infty) = k'_{ij}(+\infty) = 0$ *for* $i \neq j$. *Then* $m = 1$.

This corollary generalizes a result of Walther [7].

PROOF. Several integrations by parts show that

$$C_{ij}(r) := \int_0^\infty k_{ij}(t) \cos rt \, dt$$

$$= -r^{-2} \int_0^\infty k''_{ij}(t)(\cos rt - 1) \, dt > 0$$

$$S_{ij}(r) := \int_0^\infty k_{ij}(t) \sin rt \, dt$$

$$= -r^{-1} \int_0^\infty k'_{ij}(t)(1 - \cos rt) \, dt > 0$$

for all $r > 0$ and $i \neq j$. Clearly $|\operatorname{Im} p_\infty(ir)| \leqq \alpha$ for all r. Now

$$\operatorname{Re} p_\infty(+i\infty) = -\infty, \quad p_\infty(0) = \alpha > 0,$$

$$-\infty < \operatorname{Im} p_\infty(ir) = -\alpha(C_{12}(r)S_{21}(r)$$

$$+ C_{21}(r)S_{12}(r)) < 0, \ r > 0,$$

imply that $\arg p_\infty(+i\infty) = -\pi$ or in other words $m = 1$.

This lemma and its corollary apply for example to delay versions of the famous Volterra-Lotka model in which $f_1 = b_1 - a_{12}x_2$ and $f_2 = -b_2 + a_{21}x_1$ and for which the equilibrium is accordingly "usual-ly" unstable, for even very "weak" delays.

The author has not been able to construct kernels such that $m = -1$ in the lemma and hence for which a delay predator-prey model with infinite prey resouce has a stable equilibrium.

Now we turn our attention to the original predator-prey model (S) under the hypotheses (H1–3) and with the linearization (L). Let

$$(2) \qquad \alpha = e_1(+\infty)e_2(+\infty)a_{12}(+\infty)a_{21}(+\infty) > 0$$

in $p_\infty(z)$. If $p_\infty(z)$ satisfies the hypotheses of the lemma and $m \geqq 1$, then $p_\infty(z)$ has a finite number of roots in the right half plane $\operatorname{Re} z > 0$. Choose $R > 0$ so large that all of these roots lie *inside* the semi-circle $S(R) = \{z : |z| < R, \ \operatorname{Re} z > 0\}$ whose boundary we denote by $\partial S(R)$. Then $M = \min_{\partial S(R)} |p_\infty(z)| > 0$. From $|k^*_{ij}(z)| \leqq 1$ for $\operatorname{Re} z \geqq 0$ and the fact that α is independent of $c \geqq c_0$ it follows that

$$p(z, \ c) - p_{\infty}(z) = e_1 a_{11} z k_{11}^{*}(z)$$
$$+ \ (e_1 e_2 a_{12} a_{21} - \alpha) \, k_{21}^{*}(z)$$

tends to zero uniformly on the closure of $S(R)$ as $c \rightarrow +\infty$ (since $a_{11}(+\infty) = 0$). Thus for c large enough,

$$|p(z, \ c) \ - \ p_{\infty}(z)| < M \leqq |p_{\infty}(z)|, \ z \in \partial S(R),$$

and it follows from Rouche's theorem that $p(z, \ c)$ has roots inside $S(R)$. We have proved the following result.

THEOREM 1. *Suppose that the response functionals* f_i *in* (S) *satisfy* (H1–3) *and that the delay kernels satisfy* (H4). *If* $p_{\infty}(z)$ *with* α *given by* (2) *satisfies the hypotheses of the lemma with* $m \geqq 1$, *then for all sufficiently large inherent prey equilibria* c *the positive equilibrium* $N_i = e_i(c)$ *of the delay predator-prey system* (S) *is unstable.*

Inasmuch as the hypotheses on p_{∞} in this theorem (i.e., the lemma) are "usually" fulfilled for delay kernels satisfying (H4) as pointed out above (even for "weak" delays as in the corollary), this theorem says roughly speaking that predator-prey equilibria become unstable when the inherent prey equilibrium is large. This "enrichment paradox" is in complete accord with that stated by Rosenszweig [6] for nondelay models. Our result can apply to models for which the nondelay version has stable equilibria even for all c; for example, when the f_i are given by the linear expressions (1). Thus, *large inherent prey equilibria and the presence of even weak response delays lead to instabilities in predator-prey interactions.* Note that nothing has been assumed about the stability or instability of the inherent prey equilibrium c. It may be stable (in which case it would be called "carrying capacity") or unstable. The latter case can occur for example because of significant response delays in the prey growth rate response to its own density (as for example in he delayed logistic equation [3, Chapters 3 and 5]).

Finally we consider the case when c is close to its minimal value c_0. Here we have to distinguish two cases, depending upon the stability or instability of the inherent prey equilibrium $e_1(c_0) = c_0$ as a solution of the prey equation

$$N_1{}' = N_1 f_1 \left(\ \int_{-\infty}^{t} N_1(s) k_{11}(t - s) \, ds, \ 0; \ c_0 \ \right)$$

which governs the growth of prey in the absence of predators when $c \doteq c_0$. This equation when linearized at $N_1 = c_0$ results in a characteristic function

$$p_0(z) : \ = z + c_0 a_{11}(c_0) k_{11}^{*}(z).$$

THEOREM 2. *Assume* (H1–4). *Suppose that the inherent prey equilibrium c_0 is stable, i.e., that $p_0(z) \neq 0$ for $\mathrm{Re}\, z \geqq 0$. Then for $c > c_0$ sufficiently close to c_0 the positive equilibrium $e_i(c)$ of the delay predator-prey system (S) is (locally) asymptotically stable.*

PROOF. We will show $p(z, c) \neq 0$ for all $\mathrm{Re}\, z \geqq 0$ and $c > c_0$ close to c_0. For purposes of contradiction suppose that $p(z, c)$ has a root z_n with $\mathrm{Re}\, z_n \geqq 0$ for certain $c = c_n > c_0$ such that $c_n \to c_0$. Since $|k_{ij}(z)| \leqq 1$ for $\mathrm{Re}\, z \geqq 0$ we see from the boundedness of $e_i(c)$ and $a_{ij}(c)$ in c and from the definition of $p(z, c)$ that z_n cannot be unbounded. Thus (extracting a subsequence if necessary) we assume that $z_n \to z_0$ where of course $\mathrm{Re}\, z_0 \geqq 0$. Now by (H4)

$$0 = \lim_{n \to +\infty} p(z_n, c_n) = z_0 p_0(z_0)$$

which by assumption implies $z_0 = 0$. Thus we have sequences such that

(3) $c_n > c_0,\ c_n \to c_0,\ z_n \to 0,\ \mathrm{Re}\, z_n \geqq 0,\ p(z_n, c_n) = 0.$

We will reach the desired contradiction by showing that (3) is at odds with the implicit function theorem.

The facts that $p(0, c_0) = 0$, $p_z(0, c_0) = c_0 a_{11}(c_0) > 0$ imply the existence of a local, *unique* solution branch $z = z(c)$ of $p(z, c) = 0$ satisfying $z(c_0) = 0$. An implicit differentiation and (H4) show that

$$z'(c_0) = -e_2'(c_0) a_{12}(c_0) a_{21}(c_0) / a_{11}(c_0) < 0$$

which implies that for $c > c_0$ near c_0 the only solutions of $p(z, c) = 0$ near $z = 0$ satisfy $\mathrm{Re}\, z < 0$, in contradiction to (3).

THEOREM 3. *Assume* (H1–4). *Suppose that the inherent prey equilibrium c_0 is unstable; i.e., that $p_0(z) = 0$ has at least one root satisfying $\mathrm{Re}\, z > 0$. Then for $c > c_0$ sufficiently close to c_0 the predator-prey equilibrium $e_i(c)$ is also unstable.*

PROOF. Suppose $R > 0$ is a real such that $p_0(z)$ has a root with $\mathrm{Re}\, z > 0$ and $|z| < R$, but such that there is no root $\mathrm{Re}\, z > 0$ satisfying $|z| = R$. Since $p_0(z)$ is analytic (and not identically zero) it cannot have a root on every line segment $a + bi$, $|b| \leqq R$ for all small $a > 0$. Thus we construct a region $T(R) = \{z : \mathrm{Re}\, z > a,\ |z| < R\}$ whose boundary $\partial T(R)$ contains no root of $p_0(z)$ but whose interior does. Let $M = \min_{\partial T(R)} |p_0(z)|$. Then $M > 0$. Since

$$p(z, c) - p_0(z) = z(e_1 a_{11} - c_0 a_{11}(c_0)) k_{11}^*(z)$$
$$+ e_1 e_2 a_{12} a_{21} k_{12}^*(z) k_{21}^*(z),$$

since $|k_{ij}(z)| \leqq 1$, $\mathrm{Re}\, z \geqq 0$ and since (H2–4) hold, we see that this difference tends uniformly to zero on $\partial T(R)$ as $c \to c_0$. Thus, for $c > c_0$ close enough to c_0, we have

$$|p(z,\, c) - p_0(z)| < M \leqq |p_0(z)|, \quad z \in \partial T(R),$$

and hence Rouche's theorem yields the existence of a root of $p(z,\, c)$ in $T(R)$ for such c.

Theorems 1 and 3 imply that if the prey species is inherently unstable at $c = c_0$ then the addition of a predator will result in an unstable interaction for both large inherent prey equilibria c and for equilibria $c > c_0$ near the unstable prey equilibrium c_0. This does not mean in general that the predator-prey interaction is unstable for all $c > c_0$ however. A specific example using the linear response functionals (1) and "generic" exponential delay kernels is given in [3, Chapter 4.4]. This observation is interesting in relationship to the debate over whether prey resource or predation of prey is the dominant feature controlling prey population sizes [4], for this observation shows that it is conceivable that the prey is unstable in the absence of predators (due, for example to a large delay in growth rate response) and that at the same time the predator-prey interaction is also unstable in unlimited prey resource situations (again due to predator and/or prey interaction response delays). This situation is possible while at the same time, for appropriate intermediate values of prey equilibria c, the predator-prey community is stable.

In the case that the minimal prey equilibrium c_0 is stable the loss of stability in the predator-prey interaction as c varies from c_0 to $+\infty$ (as seen in Theorems 1 and 2) suggests a possible bifurcation of limit cycles at some critical value of c. This can occur; for details see [1, 2, 3].

Numerically solved examples illustrating the above results can be found in [2, 3].

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