THE GLOBAL ASYMPTOTIC STABILITY OF PREY-PREDATOR SYSTEMS WITH SECOND-ORDER DISSIPATION*

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Models of biological development, evolution and control should take into account that very small numbers of cells or chemicals or individuals eventually grow into stable, large populations. The simplified two-component model used in these studies includes the following: (1) first-order decay; (2) first-order autocatalysis; (3) negative feedback; (4) positive feedback; (5) second-order decay; (6) second-order autocatalysis. A positive definite Lyapunov function is constructed and shown to have a negative definite total derivative. The stationary state \( x > 0, y > 0 \), therefore possesses global asymptotic stability. This means that sustained oscillations cannot occur. Another stationary state, \( x = y = 0 \), is shown to be unstable. This means that infinitesimally small perturbations of \( x = y = 0 \) will result in evolution of the variables to the stable stationary state. This result contrasts with that obtained with the Lotka–Volterra model in that small perturbations of \( x = y = 0 \) for that model result in sustained, oscillating excursions; the smaller the initial perturbations, the larger the excursions will be.

A simulation illustrates that stable populations of \( 10^{20} \) \( x \)'s and \( y \)'s can arise from a single \( x \) and \( y \). \( x \) grows more or less continuously, but \( y \) remains extremely small for 80 per cent of the time interval required for the variables to approach their stable populations.

Macroscopic biological events like evolution or cellular differentiation are characterized by sequences of instability, increased dimensionality, and stability. The appearance of new components is initially "spontaneous". If the

new component is to survive, it must interact with its environment, and it must
maintain itself by a replication process that balances the natural processes of
dissipation and decay. These processes, interaction, replication and decay are
incorporated into the two-component model described by equation 1:
\[
\begin{align*}
\dot{x} &= (\alpha_1 - a_1)x - bxy + (\zeta_1 - g_1)x^2 \\
\dot{y} &= (\alpha_2 - a_2)y + \beta xy + (\zeta_2 - g_2)y^2.
\end{align*}
\] (1)

Here we suppose the first-order constant for replication of x is greater than the
first-order constant for decay of x \((\alpha_1 > a_1)\), the first-order constant for decay
of y is greater than the first-order constant for replication of y \((\alpha_2 < a_2)\), and
the second-order constants for replication are less than the respective second-
order constants for decay of x or y \((\zeta_1 < g_1 \text{ and } \zeta_2 < g_2)\). The first equation
includes negative feedback control of x by y, and the second equation describes
a positive feedback by x on y.

When \(\alpha_1 > a_1\) or \(\alpha_2 > a_2\) (1) possess an unstable solution at the origin
\((Walter, 1973)\). This type of instability in the neighborhood where the variables
are small may be important in biology because it is precisely this sort of evolu-
tion of large populations from relatively small initial amounts that is so wide-
spread in biology. Since the singularity at the origin is unstable only if
\(\alpha_1 > a_1\) or \(\alpha_2 > a_2\), "self-reproduction" by at least one of the components is
necessary.

When \(g_1 > \zeta_1\) and \(g_2 > \zeta_2\) the other parameters can be chosen so that (1)
possess a singular point in the first quadrant \((x^*, y^*)\). In order to ascertain the
stability properties of this point, consider the positive definite Lyapunov
function\(^\dagger\)
\[
V = \left[\frac{x^* e^{x/x^*}}{x} \right]^{\eta} \left[\frac{y^* e^{y/y^*}}{y} \right]^\mu - e^{\eta + \mu}.
\] (2)

This function has the property, \(\lim_{x,y \to \infty} V = \infty\) \((Walter, 1972)\) which
Brashin and Krasovsky \((1952)\) have shown guarantees closure of the Lyapunov
surfaces. This point is critical for studies of global stability. For \(\eta = x^*/b\)
and \(\mu = y^*/b\) the derivative of V,
\[
-\dot{V} = \left[\frac{x^* e^{x/x^*}}{x} \right]^{\eta} \left[\frac{y^* e^{y/y^*}}{y} \right]^\mu \left[\eta(g_1 - \zeta_1) (x - x^*)^2 + \frac{\mu(g_2 - \zeta_2)}{y^*} (y - y^*)^2\right],
\] (3)
is negative definite for all \(g_1 > \zeta_1\) and \(g_2 > \zeta_2\). The singular point \((x^*, y^*)\)
therefore possesses global asymptotic stability.

The behavior of (1) is quite different from the behavior reported by Lotka

\(^\dagger\) I am indebted to Gregory Dunkel who first suggested this Lyapunov function to me in 1967.