# Elements of Mathematical Ecology

MARK KOT

*Department of Applied Mathematics,*
*University of Washington*

CAMBRIDGE
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*Theorem* Suppose that $N^*$ is an equilibrium point and that $f(N)$ is a continuously differentiable function. Suppose also that $f'(N^*) \neq 0$. Then the equilibrium point $N^*$ is asymptotically stable if $f'(N^*) < 0$, and unstable if $f'(N^*) > 0$.

*Proof* Consider an equilibrium for which $f'(N^*) < 0$ and let $x(t) \equiv N(t) - N^*$. If we expand $f(N)$ about $N^*$, we obtain

$$\frac{dx}{dt} = f(N^*) + f'(N^*)x + g(x). \tag{1.17}$$

Since $N^*$ is an equilibrium, equation (1.17) reduces to

$$\frac{dx}{dt} = f'(N^*)x + g(x), \tag{1.18}$$

which may be viewed as a perturbation of a linear, constant-coefficient differential equation. Note that $g(x)$ consists of higher-order terms. In particular, $g(x)$ satisfies $g(0) = 0$ and also $g'(0) = 0$. This, along with the continuity of $g'(x)$ (which follows from the continuity of $f'(N)$), guarantees us that for each $\epsilon > 0$ there is a small $\delta$ neighborhood about zero wherein $|g'(x)| < \epsilon$. As a result,

$$g(x) = \int_0^x g'(s)\,ds \leq \epsilon|x|. \tag{1.19}$$

It follows that

$$\frac{dx}{dt} \leq f'(N^*)x + \epsilon|x|. \tag{1.20}$$

For small enough $\delta$ and $\epsilon$ and $f'(N^*) \neq 0$, the higher-order terms cannot change the sign of $dx/dt$. As a result, small enough perturbations will decay; the equilibrium is asymptotically stable. A similar argument can be made to show that $f'(N^*) > 0$ implies instability. □

Take another look at Figure 1.5. You should be able to ascertain the stability of the two equilibria *by inspection* with this theorem. What do you think happens when $f'(N^*) = 0$?

## Historical hiatus

The concepts of exponential and logistic growth arose gradually. A few people played especially important roles in the development of these concepts.

**John Graunt** (1662) was a 'collector and classifier of facts' (Hutchinson, 1980). He was also the inventor of modern scientific demography. Graunt tabulated the Weekly Bills of Mortality for London. These bills listed births and deaths; they were used as an early warning system for the plague. Using these bills, Graunt estimated a doubling time for London of 64 years. This is an extremely short period of time. Graunt posited that if the descendants of Adam and Eve (created in 3948 BC, according to Scaliger's chronology) doubled in number every 64 years, the world should be filled with 'far more People, than are now in it.' By my calculation, this would amount to

$$2^{(1662+3948)/64} \approx 2^{87.7} \approx 2.5 \times 10^{26} \approx 200 \text{ million people/cm}^2. \tag{1.21}$$

Graunt was clearly aware of the power of exponential growth.

**Sir William Petty** (1683) faulted Graunt for ignoring the biblical flood. He started the clock with Noah ($t_0 = 2700$ BC with $N_0 = 8$). Petty also felt that Graunt's estimate for a doubling time was misleading, since much of London's increase was due to immigration. Petty estimated the doubling time for England to be between 360 and 1200 years. However, a doubling time of 360 years left Petty with a population projection,

$$8 \times 2^{12.175} \approx 36\,994, \tag{1.22}$$

that was far too small. Petty therefore proposed that the human growth rate had fallen steadily in postdiluvian times. He produced a table 'shewing how the people might have doubled in the several ages of the world'; the table exhibited a steady increase in the doubling time, much as one would expect for logistic growth.

The **Reverend Thomas Robert Malthus** (1798) is famous for having written *An Essay on the Principle of Populations.* The essence of this book may be represented with a simple quasi-equation:

$$\begin{matrix}\text{a geometrically} \\ \text{growing} \\ \text{population}\end{matrix} + \begin{matrix}\text{an arithmetically} \\ \text{growing} \\ \text{food supply}\end{matrix} = \begin{matrix}\text{much} \\ \text{human} \\ \text{misery}\end{matrix}. \tag{1.23}$$

Many of Malthus's conclusions had already been anticipated by Graunt, Petty, and others. However, Malthus is justly famous for stating the case so clearly. Malthus's book had tremendous influence on Charles Darwin and Alfred Russel Wallace and, in effect, provided them with the material basis for natural selection.

**Pierre-François Verhulst** (1845) was a Belgian who presented an entirely modern derivation of the logistic equation. His work went unappreciated during his own lifetime and he died in relative obscurity.

**Raymond Pearl** and **Lowell Reed** (1920) rediscovered the logistic equation and launched a crusade to make the logistic equation a 'law of nature' (Kingsland, 1985). They published over a dozen papers between 1920 and 1927 promulgating this law. Some of their extrapolations and *ad hoc* pastings of logistic curves were questionable, but they did make the logistic equation famous.

The logistic equation allows us to handle limited growth in a natural way. This equation also has a long history. However, there is nothing sacred about this equation. Other models, derived differently, exhibit many of the same properties.