Chapter 10
Lotka and stable population theory (1907–1911)

Alfred James Lotka was born of American parents in 1880 in Lemberg, which was part of the Austro-Hungarian Empire (now L’viv in Ukraine). He studied first in France and Germany and in 1901 obtained a bachelor’s degree in physics and chemistry from the University of Birmingham in England. He then spent one year in Leipzig where the role of thermodynamics in chemistry and biology was emphasized by Wilhelm Ostwald, who was to receive the Nobel prize in Chemistry in 1909. Lotka settled in New York in 1902 and began to work for the General Chemical Company.

Fig. 10.1 Lotka (1880–1949)

In 1907 and 1911\(^1\), Lotka took up the study of the dynamics of age-structured populations without knowing about Euler’s work on the same subject (see Chapter 3). Unlike Euler he assumed that time and age are continuous variables. Let \(B(t)\) be the male birth rate (the number of male births per unit of time) at time \(t\), \(p(x)\) the probability of being still alive at age \(x\) and \(h(x)\) the fertility at age \(x\): \(h(x)\,dx\) is

\(^1\) The second article was written in collaboration with F.R. Sharpe, a mathematician from Cornell University.
the probability for a man to have one newborn son between age $x$ and $x + dx$ if $dx$ is infinitely small. Then

$$\int_0^\infty p(x) \, dx$$

is the life expectancy at birth. Moreover $B(t - x) \, p(x) \, dx$ is the number of males born between time $t - x$ and $t - x + dx$, which are still alive at time $t$. These males have $B(t - x) \, p(x) \, h(x) \, dx$ sons per unit of time at time $t$. So the total male birth rate at time $t$ is

$$B(t) = \int_0^\infty B(t - x) \, p(x) \, h(x) \, dx.$$

Looking for an exponential solution for this integral equation in the unknown $B(t)$ of the form $B(t) = b \, e^{rt}$, Lotka obtained by dividing both sides by $B(t)$ the equation

$$1 = \int_0^\infty e^{-rx} \, p(x) \, h(x) \, dx,$$

which is now called “Lotka’s equation” by demographers. Euler had obtained the analogous implicit equation (3.1) for the growth rate when time and age are discrete variables. Lotka noticed that the right-hand side of (10.1) is a decreasing function of $r$ which tends to $+\infty$ when $r \to -\infty$ and which tends to 0 when $r \to +\infty$. So there is a unique value of $r$, call it $r^*$, such that equation (10.1) holds. Besides, $r^* > 0$ if and only if

$$R_0 = \int_0^\infty p(x) \, h(x) \, dx > 1.$$  

(10.2)

The parameter $R_0$ (the notation was introduced by Dublin and Lotka in 1925) is the expected number of sons that one man may have throughout his life.

Lotka suggested that, whatever the initial age structure of the population, the number of male births per unit of time was indeed such that $B(t) \sim b \, e^{rt}$ when $t \to +\infty$, where $b$ is a constant. The total population is then given by

$$P(t) = \int_0^\infty B(t - x) \, p(x) \, dx.$$

It follows that $P(t)$ also increases or decreases like $e^{rt}$ when $t \to +\infty$; the growth rate is equal to $r^*$. Moreover, the population’s age structure, given by $B(t - x) \, p(x) / P(t)$, tends to

$$\frac{e^{-r^*x} \, p(x)}{\int_0^\infty e^{-r^*y} \, p(y) \, dy}.$$

This is what Lotka called a “stable population”: the age pyramid keeps the same shape through time but the total population increases or decreases exponentially.

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2 R.A. Fisher arrived independently at the same equation in 1927 and later interpreted the root $r^*$ as a measure of “Darwinian fitness” in the theory of evolution by natural selection.

3 This was rigorously proven in 1941 by Willy Feller, who was then professor of mathematics at Brown University in the USA. A probabilistic approach was developed in 1968 by Crump, Mode and Jagers.