LECTURE 3

Population Dynamics

The simplest of all the growth processes which provide models for population dynamics is exponential growth. This is a process of constant proportional growth whereby each time period witnesses the same percentage increase in numbers. If the proportional rate of growth ρ is constant; and, if $\rho > 0$, then the absolute rate of growth must be ever-increasing. When $\rho < 0$, there is a constant proportional rate of decline in the population and a diminishing absolute rate. A zero population is approached as time elapses, but it is never reached.

Let $y \geq 0$ represent the size of the population which, for convenience, we take to be a real number instead of an integer. Then the differential equation governing exponential growth is

$$\frac{dy}{dt} = \rho y, \tag{1}$$

where t stands for time. The solution of the equation is the exponential function

$$y = y_0 e^{\rho t}, \tag{2}$$

where y_0, which stands for the size of the population at time $t = 0$, is described as the initial condition, and where $e \simeq 2.7183$ is the so-called natural number. To confirm that this function satisfies the differential equation, we simply differentiate it via the chain rule to obtain $dy/dt = \rho y_0 e^{\rho t} = \rho y$.

To find the value of y at time t when ρ and y_0 are given, we may take natural logarithms—ie. logs to the base e—of equation (2) to give

$$\ln y = \ln y_0 + \rho t. \tag{3}$$

Once the value of $\ln y$ has been calculated, the value of y may be recovered from a table of antilogarithms. We can also use logs to the base 10. In that case, we have

$$\log_{10} y = \log_{10} y_0 + (\log_{10} e)\rho t. \tag{4}$$

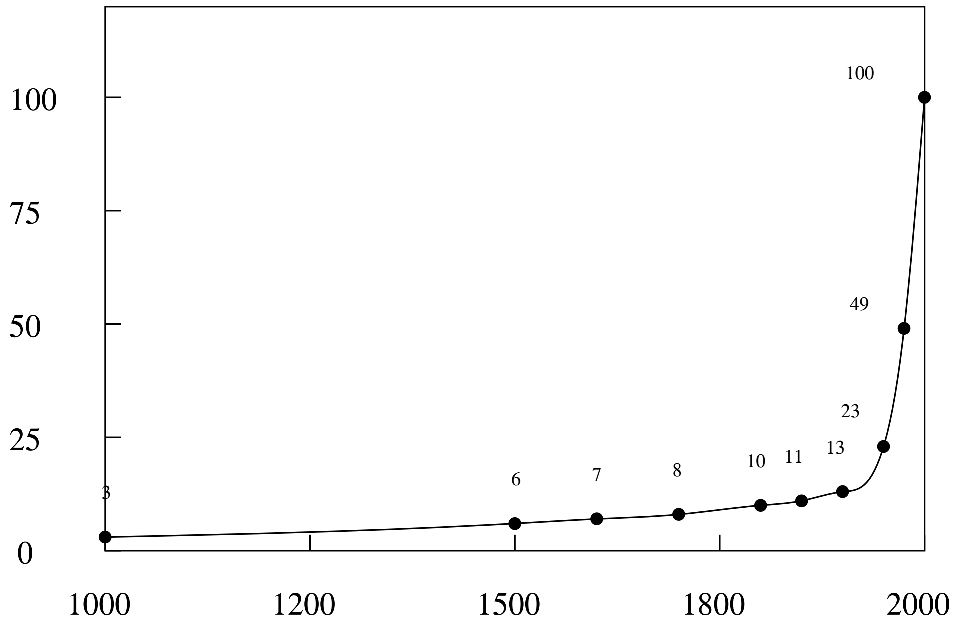


Figure 1. The population in millions of East Africa, comprising the countries of Uganda, Kenya, Tanzania and Rwanda and Burundi.

Whatever of the base of the logarithms, the log of an exponential function is a linear function of t.

Example. Some of the highest rates of population growth are to be found in East Africa. In 1950, the population in the area which now comprises Kenya, Uganda and Tanzania was estimated at 23 million. By 1975, this had become 49 million. We may use the formula $\rho = (\ln y - \ln y_0)/t$ in showing that

$$\begin{aligned} y &= y_0 e^{\rho t} \\ &= 23,000,000 \times e^{(0.03025 \times 25)} \\ &= 49,000,000, \end{aligned} \tag{5}$$

which indicates that the growth rate was in excess of 3% per annum. To get the measure of this rate of increase, we may calculate that, if it were it to continue, there would be 104.39 million people by the turn of the century 222.40 million by 2025 and 473.81 million by 2050. That is to say, by the year 2050, the East African population would equal that of China in the year 1900 and it would exceed the Indian population of the year 1975. These numbers are impossible; and an epidemic of AIDS has already supervened which seems bound to retard the growth of population.

For some purposes, it is simpler to analyse the growth of population in terms of discrete-time models which generate a sequences of values instead of a continuous trajectories. The discrete-time analogue of exponential growth is geometric growth which is represented by the equation

$$y_t = y_0(1+r)^t. \tag{6}$$

On comparing equations (2) and (6), we find that $y_t/y_0 = (1+r)^t = e^{\rho t}$; which indicates that $1+r = e^{\rho}$. The exponential and the geometric rates, which are denoted by ρ and r respectively, differ with $r > \rho$. However, the geometric rate tends to the exponential rate as the length of the unit time period decreases.

To demonstrate the convergence of geometric and exponential growth, and to discover a means of evaluating the natural number, we can take the analogy of the growth of a fixed-interest financial investment. The aim is to determine the effect of compounding the earnings with the capital at ever-decreasing intervals of time.

If the earnings were compounded with the investment twice a year, then the growth factor would be $(1+\frac{1}{2}r)^2$. If they were compounded ever quarter, the factor would be $(1+\frac{1}{4}r)^4$. If the earnings were compounded continuously, then the growth factor would be $\lim(n\rightarrow\infty)(1+\frac{r}{n})^n$. To evaluate this limit, we may expand the expression in a power series Recall that, according to the binomial theorem,

$$\begin{aligned}(a+b)^n = a^n + na^{n-1}b + \frac{n(n-1)}{2}a^{n-2}b^2 + \frac{n(n-1)(n-2)}{3!}a^{n-3}b^3 \\ + \cdots + \frac{n(n-1)}{2}a^2b^{n-2} + nab^{n-1} + b^n.\end{aligned} \tag{7}$$

This indicates that

$$\left(1+\frac{r}{n}\right)^n = \left\{1 + n\frac{r}{n} + \frac{n(n-1)}{2}\frac{r^2}{n^2} + \frac{n(n-1)(n-2)}{3!}\frac{r^3}{n^3} + \cdots\right\}. \tag{8}$$

The consequence is that

$$\lim_{n\rightarrow\infty}\left(1+\frac{r}{n}\right)^n = \left\{1 + r + \frac{r^2}{2!} + \frac{r^3}{3!} + \cdots\right\}. \tag{9}$$

Setting $r = 1$ in this expression gives

$$\begin{aligned}\lim_{n\rightarrow\infty} = \left(1+\frac{1}{n}\right)^n = \left\{1 + 1 + \frac{1}{2!} + \frac{1}{3!} + \cdots\right\} \\ = e,\end{aligned} \tag{10}$$

and this provides the means of calculating the natural number to any desired degree of accuracy. Finally, by defining $q = n/r$ and by observing that, if r is fixed, then $q \to \infty$ as $n \to \infty$, we can see that

$$\lim_{n\to\infty}\left(1+\frac{r}{n}\right)^n = \left\{\lim_{q\to\infty}\left(1+\frac{1}{q}\right)^q\right\}^r = e^r. \tag{11}$$

Logistic Growth

The rate of increase in a population is the difference between the rate of addition of individuals due to birth B and immigration I and the rate of loss due to death D and emigration E:

$$\frac{dy}{dt} = B + I - D - E. \tag{12}$$

Matters are simplified if, for a start, we consider a closed population with $I = E = 0$. In most models which are of any interest, the rates of birth and death are functionally related to the size y of the population itself. This is certainly true in the case of exponential growth were the births and deaths are assumed to be directly proportional to y. Thus, with $B = \beta y$ and $D = \delta y$, we have

$$\frac{dy}{dt} = \beta y - \delta y = \rho y, \tag{13}$$

where $\rho = \beta - \delta$. In the closed population, any increase is due entirely to the excess of births over deaths.

It is only in rare cases and for short periods that a population can follow an exponential growth path. Very soon a scarcity of resources or of space, and perhaps an increasing problem of environmental pollution, will slow or arrest the growth. The effect will be achieved either via a decline in the birth rate β or an increase in the death rate δ or in both of these ways. A simple notion is to postulate that the birth rate is a declining linear function of y and that the death rate is an increasing linear function of y:

$$\begin{aligned} \beta &= \lambda_0 + \lambda_1 y, \qquad \lambda_1 < 0 \\ \delta &= \mu_0 + \mu_1 y, \qquad \mu_1 > 0. \end{aligned} \tag{14}$$

In that case, there will be a certain population size, say $\bar{y}$, where the numbers of births and deaths are equal. Thus, if

$$\lambda_0 + \lambda_1 \bar{y} = \mu_0 + \mu_1 \bar{y}, \tag{15}$$

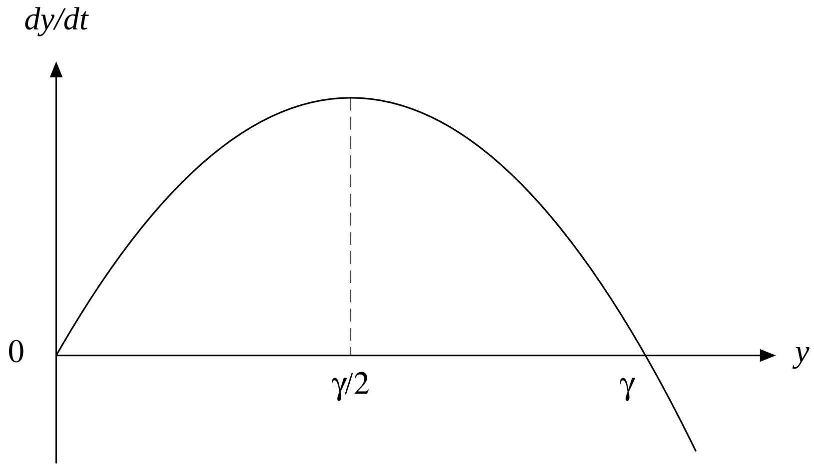


Figure 2. The growth rate in the logistic model.

then

$$\bar{y} = \frac{\lambda_0 - \mu_0}{\mu_1 - \lambda_1}. \tag{16}$$

Amongst ecologists, this population level is described as the carrying capacity of the environment. It is useful to adopt special symbols both for the carrying capacity and for the differential between births and deaths at the point where $y = 0$:

$$\gamma = \frac{\lambda_0 - \mu_0}{\mu_1 - \lambda_1}, \qquad \rho = \lambda_0 - \mu_0. \tag{17}$$

In these terms, the rate of growth of the population is given by

$$\begin{aligned} \frac{dy}{dt} &= (\beta - \delta)y \\ &= \rho y \left(\frac{\gamma - y}{\gamma} \right). \end{aligned} \tag{18}$$

The expression on the RHS stands for a quadratic function of y whose curve passes through the origin and reaches a maximum at $y = \gamma/2$. This is the so-called logistic model of population growth which is also called the Verhulst–Pearl model.

It is easy to interpret the logistic model which is merely the exponential model of (1) modified by the factor $(\gamma - y)/\gamma$. To understand the effect of

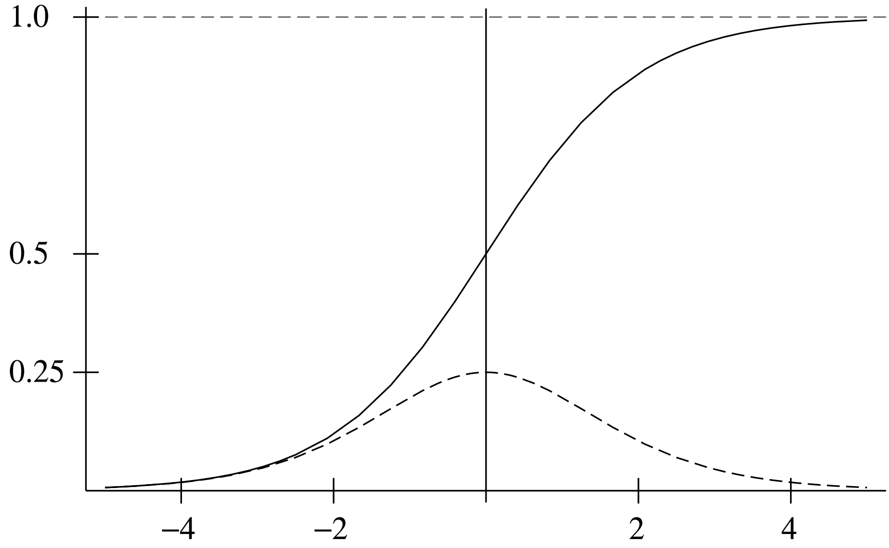


Figure 3. The Logistic function $y = 1/(1 + e^{-t})$ and its derivative. For large negative values of t, the function and its derivative are close. In the case of the exponential function $y = e^t$, they coincide for all values of t.

this factor, imagine that y is close to zero. Then the value of the factor will be close to unity and the process of growth will be almost exponential. Now imagine that $y = \gamma$, which is to say that the population has reached the carrying capacity of the environment. Then the factor will have the value of zero and there will be no population growth.

The model does not preclude the case where $y > \gamma$. In that case $dy/dt < 0$, and the population will decline toward the level of γ. However, there might be a need to explain how the population has come to exceed the carrying capacity of the environment. The excess population might be due to immigration or it might be due to a reduction that has occurred in the carrying capacity.

The logistic model is uncommon amongst continuous-time models of population dynamics in that its trajectory can be represented by a simple analytic function. Usually such trajectories have to be calculated by a process of numerical integration. The form of the solution for the logistic model depends upon whether the carrying capacity, which represents the steady-state asymptote of the dynamic system, is being approached from above or below. Assuming that $y < \gamma$, the general solution is given by the equation

(19) $$y = \frac{\gamma}{1 + e^{\alpha - \rho t}}.$$

The graph of the function for some some special and simplifying choices of γ, ρ and α is presented in Figure 3. There is no great loss of generality in setting $\gamma = 1$ and $\alpha = 0$. When $\gamma = 1$, the equation represents the size of the population as a proportion of the carrying capacity. Setting $\alpha = 0$ establishes a new time origin which predates the former origin of t by α/ρ periods.

To confirm that the function of (19) does satisfy equation (18), we need to differentiate it:

$$\begin{aligned}\frac{dy}{dt} &= \frac{\gamma\rho e^{\alpha-\rho t}}{(1+e^{\alpha-\rho t})^2} \\ &= \rho y \frac{e^{\alpha-\rho t}}{1+e^{\alpha-\rho t}}.\end{aligned} \tag{20}$$

Then it only remains to be confirm that

$$\frac{e^{\alpha-\rho t}}{1+e^{\alpha-\rho t}} = \frac{\gamma - y}{\gamma}, \tag{21}$$

which is easily done.

Interpretations of The Logistic Model

In spite of its simplicity, the logistic model can bear the weight of a good deal of interpretation; and, at the same time, it tends to suggest several avenues for further enquiry.

Density Effects. The basic issues which are raised by the model concern the dependence of the birth and death rates on the population size. If we imagine that the population is confined to a limited area, then the reactions to population changes can be described as density-dependent effects.

The density effects constitute an equilibrating mechanism which guides the population towards the level of γ. The effects may be largely attributable to the environment or they may be the consequence of self-regulating mechanisms which are inherent in the species.

A high density can have an effect upon mortality by limiting the per-capita food supply, thereby debilitating the individuals and leaving them prone to the ravages of disease and famine. It may also affect fertility which is liable to be lower in unhealthy and malnourished individuals than in healthy and well-fed ones. In connection with human populations, these effects are described as Malthusian mechanisms.

There may be other, more salutary mechanisms, which limit fertility in cases of high population density. In some species of animals, the chemical secretions or the sexual displays which are the prelude to mating are not so forthcoming in crowded conditions, and these suppressions may be regarded as instances of self-regulating mechanisms.

In the case of human populations, one may have to look carefully to discover the self-regulating mechanisms. Even if the stress of living in crowded conditions is unlikely to effect human fertility for physical reasons, it may well affect it for social reasons. Thus, for example, the presence of a mother-in-law in the same dwelling may have a depressive effect upon the fertility of a young married couple. This may be a factor in the comparatively low fertility rates of some Eastern European countries which have long been affected by housing shortages.

When we recognise that the global human population is increasing at an unsustainable rate, we are bound to wonder whether the growth will be halted by a decline in the birth rate or by a rise in the death rate, or by both. In almost every case, the current high rates of increase are due to a fall in the death rate bought about, almost exclusively, by a fall in infant mortality. The hope has been that the birth rate in third-world countries would follow the downward trend of the death rate, with a brief time-lag, as it has done in the developed countries. To date, there is little evidence of such a decline; and there is fear that time is running out.

Extinctions. It is fair to say that populations whose evolution is not governed by density-dependent effects are in danger of an early extinction. The numbers in such populations will drift widely under the impact of favourable and adverse environmental circumstances. If their birth rate is not liable to rise and their death rate to fall in conditions of low population density, then they might not be able to respond adequately to an environmental shock which depletes their numbers.

In this connection, the logistic model is undoubtedly an over-simplification, for it suggests that the rate of increase is greatest at times when the population density is lowest, which is when the population is on the verge of extinction. In such circumstances, the species may suffer from several additional disadvantages. In the first place, mature individuals might have difficulty in finding mates if the density is too low. In the second place, level of fertility may be adversely affected by inbreeding which can lead to a loss of genetic diversity and to an increased likelihood that the offspring will inherit two copies of a defective recessive gene. Also, populations which lack genetic diversity run a risk of succumbing, en masse, to a single disease.

A simple elaboration of the logistic model is available which incorporates a lower limit or survival threshold κ, below which growth is negative and the species heads for extinction. The modified model simply incorporates an additional factor so that the equation becomes

$$\frac{dy}{dt} = \rho y \left(\frac{\gamma - y}{\gamma}\right)\left(\frac{y - \kappa}{y}\right). \tag{22}$$

The function of the RHS of (22) is a quadratic; but, in contrast to the function under (18), its curve does not pass through the origin. Instead, it cuts the horizontal axis at a positive value of $y = \kappa$. The extinction effect comes into

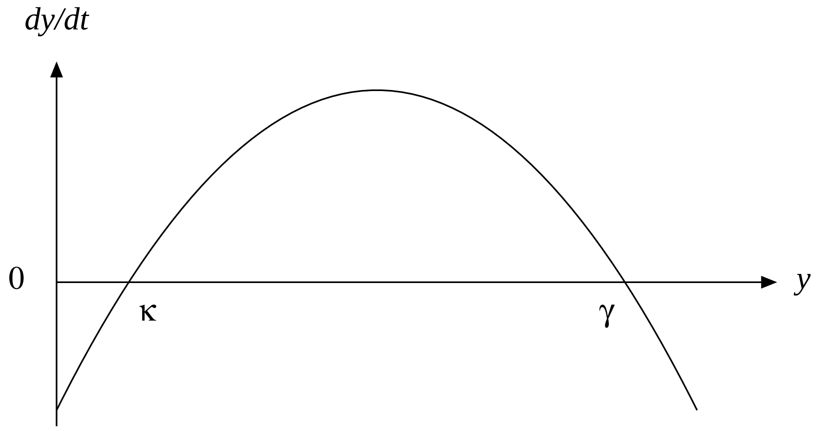


Figure 4. The growth function of a modified logistic model incorporating a survival threshold.

operation when y falls below κ, since the additional factor is then negative. For values of y which are significantly larger than κ, the effect of the factor is slight; for, in those cases, it does not differ greatly from unity.

It should be understood that, in common with $y = \gamma$, the population level of $y = \kappa$ represents a point of equilibrium. However, it differs from γ in that it represents an *unstable* equilibrium. If the population falls below κ, then a process of decline is set in motion which drives it to extinction. If it exceeds κ, then a process of growth is set in motion which will carry the population towards the stable equilibrium point of γ.

The Population Strategies of the Species. In some ways, it is misleading to describe the parameter γ of (17) as the carrying capacity of the environment, since it is as much a function of the vital parameters which govern the birth and death rates of the species as it is of the environments in which they live.

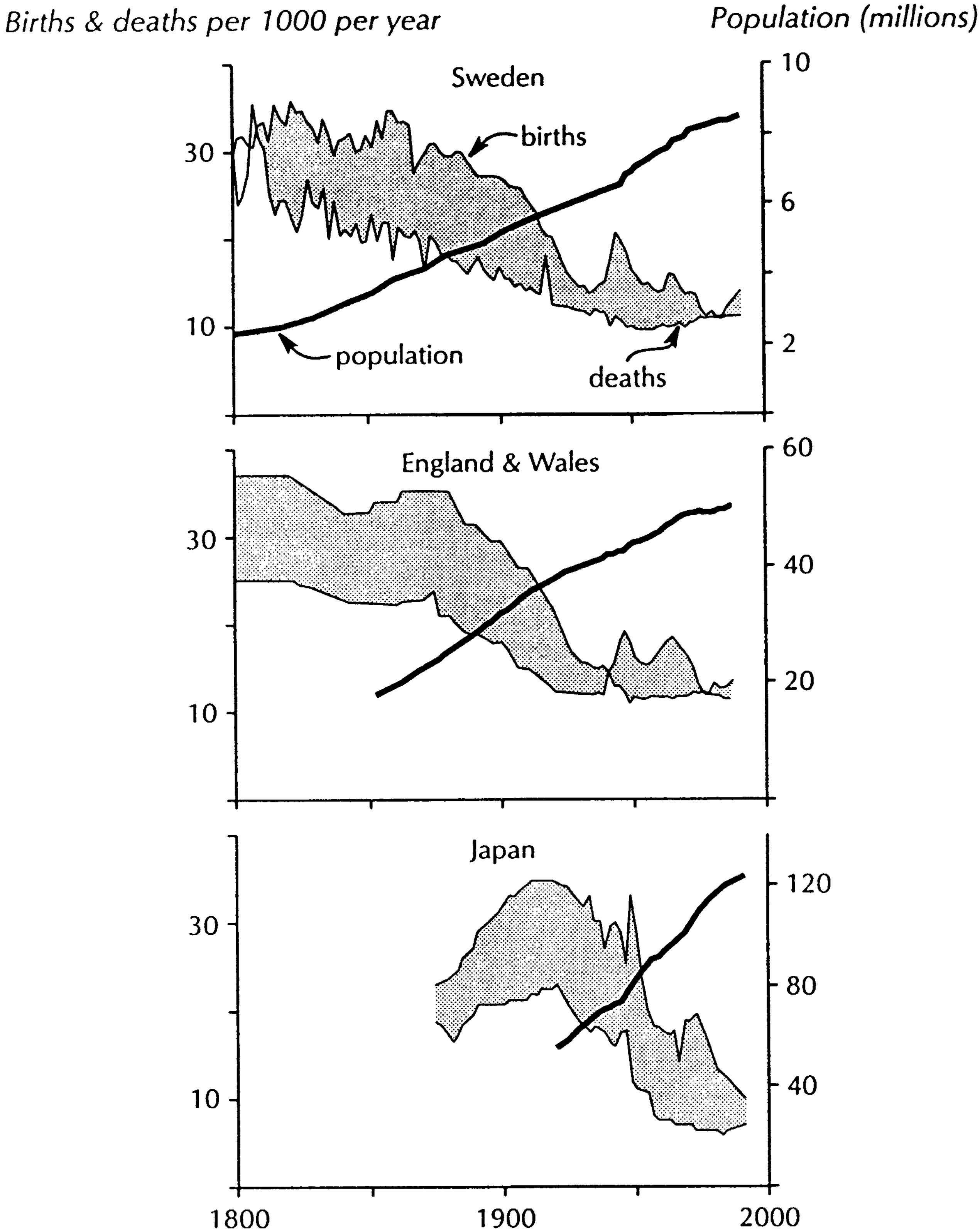
In a given environment, the parameters ρ and γ, are determined by the genetics of the individuals. Therefore, it is natural to suppose that they have been subject to a process of evolution governed by natural selection. In this way, one might be able to account for some of the wide variety of population sizes and inherent growth rates found amongst the species.

Some species are adapted to live in ephemeral environments from which they must emigrate in large numbers at birth or shortly afterwards. Such species are likely to have a high inherent growth rate ρ which should enable them rapidly to colonise favourable environments as well as to sustain the high rates of mortality to which they are subject whilst migrating to new habitats.

Other species are adapted to live in stable and specialised environments where territories can be found which individuals or groups can demarcate and preserve. These species are liable to be longer-lived than others; and their reproductive rates are liable to be lower. A good example is provided by the forest-dwelling gorillas whose low reproductive rates now pose a threat to their survival as the extent of their natural habitat is reduced by the incursions of man.

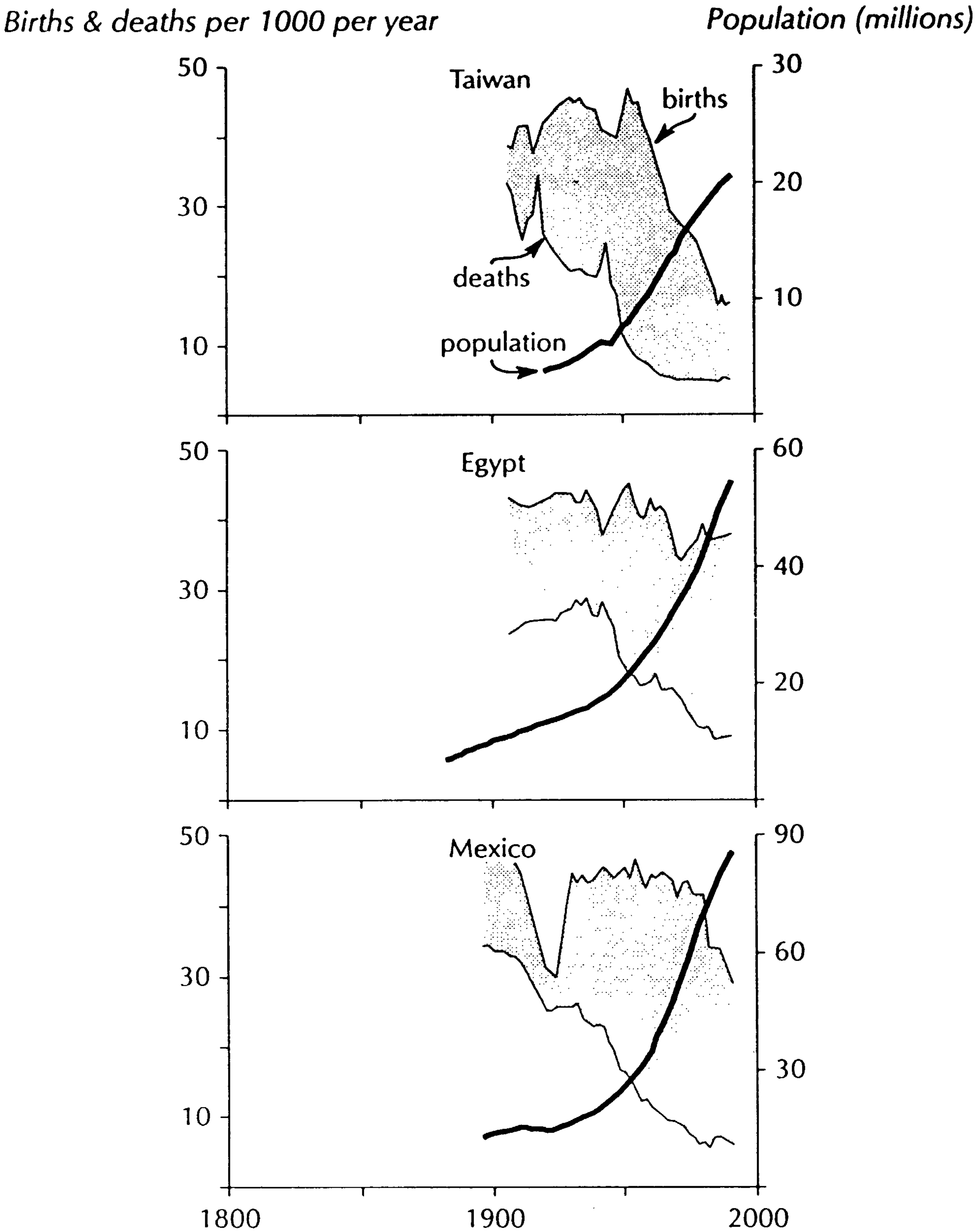
The case can be made that the natural fertility of mankind represents an adaptation to circumstances which no longer characterise our lives. Our fertility rates may have been established at a time when man's hominid forebears were in the process of dispersing over much wider areas than those inhabited by their simian ancestors. The ancestral habitats may have resembled those of the modern gorilla and the chimpanzee. According to this supposition, the high fertility rates, which were established at the time of the dispersal, are the feature which has caused the populations of mankind, since time immemorial, to press so relentlessly against the limits of the available resources.

Figure 2-6a DEMOGRAPHIC TRANSITIONS IN INDUSTRIALIZED COUNTRIES



In the demographic transition a nation's death rate falls first, followed later by its birth rate. Sweden's demographic transition occurred over almost 200 years, with the birth rate remaining rather close to the death rate. During this time Sweden's population increased less than fivefold. Japan is an example of a a nation that will effect the transition in less than a century. The less-industrialized countries have

Figure 2-6b DEMOGRAPHIC TRANSITIONS IN LESS-INDUSTRIALIZED COUNTRIES



less time to accomplish this shift, and the gaps between their birth and death rates are larger than any that prevailed in the long-industrialized countries. (*Sources: United Nations; R. A. Easterlin; J. Chesnais; N. Keyfitz; Population Reference Bureau; U.K. Office of Population Census and Surveys.*)