Verhulst's Logistic Curve

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Students tend to regard the elongated "S-shaped" logistic curve of population dynamics (Figure 1) as somewhat exotic. It is typically derived by applying the method of partial fractions to a separable differential equation. My purpose here is to show how the logistic curve may be derived more directly as a simple consequence of the more familiar differential equation model for exponential decay, and that the curve itself is nothing more than a familiar friend in disguise. The disguise is removed by abandoning our fixation on the reference point $(0, P_0)$, representing the initial population at time zero, in favor of a more natural choice. This illustrates an important principle, namely that one should always adapt the coordinates to the problem at hand. In this case, a great deal is simplified by relocating the origin more appropriately.

Textbooks typically begin the discussion of population growth with the exponential model

$$\frac{1}{P}\frac{dP}{dt} = k \qquad \Longrightarrow \qquad P(t) = P_0 e^{kt}, \qquad t \ge 0, \tag{1}$$

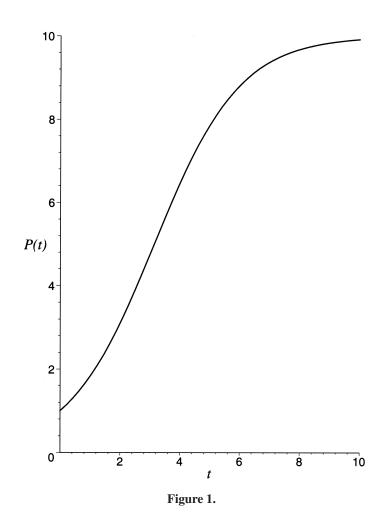
in which the relative growth rate k is a positive constant, say the average birth rate. Since unbounded growth is unrealistic, more sophisticated models take into account factors such as limited resources for reproduction. The logistic model, proposed by the Belgian mathematical biologist Pierre F. Verhulst in 1838 [1], replaces the constant relative growth rate in (1) with a relative growth rate that decreases linearly as a function of P:

$$\frac{1}{P}\frac{dP}{dt} = k\left(1 - \frac{P}{M}\right), \qquad k > 0, \qquad 0 < P_0 < M.$$
⁽²⁾

The constant *M* represents the maximum sustainable population beyond which *P* cannot increase. The dimensionless factor 1 - P/M in (2) serves to diminish the relative growth rate from *k* down to zero as the population increases from its initial level P_0 to *M*.

Although one can solve (2) as a Bernoulli differential equation by making the substitution P = 1/y, for the most part texts treat (2) as a separable differential equation to be solved by the method of partial fractions. Either way, one obtains, after some algebraic simplifications, the solution

$$P(t) = \frac{M}{1 + R_0 e^{-kt}}, \quad \text{where} \quad R_0 = \frac{M - P_0}{P_0}.$$
 (3)



For the instructor who would like to discuss logistic growth but would prefer to bypass partial fractions, an alternative approach is called for. Suppose instead of counting individuals, we count niches, viewing M as the maximum number of niches the ecosystem can support, and P as the number of niches currently occupied. Dimensional analysis suggests that instead of studying P, we consider

$$R = \frac{M - P}{P},\tag{4}$$

the dimensionless ratio of available or vacant niches to niches currently occupied. We will dispense with (2) and instead make the simpler exponential decay differential equation

$$\frac{1}{R}\frac{dR}{dt} = -k, \qquad k > 0, \qquad 0 < R_0 < \infty$$
⁽⁵⁾

an *assumption of the model*. An obvious advantage of this approach is that solving (5) is trivial. We get

$$R(t) = R_0 e^{-kt},\tag{6}$$

which with the help of (4) is easily solved for P to obtain (3).

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A related aspect the approach via (4) and (5) we are proposing has in its favor is that logistic growth can be introduced in the standard section on exponential growth and decay, with no loss in continuity and without any additional background. That R decreases at a rate proportional to itself, i.e., satisfies the differential equation (5), is intuitively plausible. Initially we think of P being much smaller than M, so that R is much larger than 1 and many niches are available relative to the number currently occupied (a high niche vacancy rate). We should expect any species to take advantage of such a hospitable climate for reproduction, and hence initially, R should decrease rapidly as P increases. However, as the number of vacancies decreases, (P gets close to M, R gets close to zero) there are relatively few available niches remaining. In such an *inhospitable* climate, we should ecrease much more slowly. These considerations should be sufficient to motivate the introduction of logistic growth via (4) and (5) to any calculus or differential equations class. (Of course (5) could also be derived from (2) with little difficulty.)

From the viewpoint of an individual of the species attempting to reproduce, one should expect a qualitative change in the hospitality of the ecosystem near R = 1, given the considerations of the previous paragraph. Motivated by these considerations, we refer to an ecosystem as being *hospitable* or *inhospitable* according to whether R is greater or less than 1. From (4) and (6), the transition from hospitable to inhospitable occurs when

$$R = 1, \qquad P = \frac{1}{2}M, \qquad t = \tau_0 := \frac{1}{k}\log R_0 = \frac{1}{k}\log\left(\frac{M - P_0}{P_0}\right). \tag{7}$$

This is precisely the time at which P is increasing most rapidly, as can be seen by completing the square in (2):

$$\frac{dP}{dt} = \frac{1}{4}Mk - \frac{k}{M}\left(P - \frac{1}{2}M\right)^2.$$

Because of the distinguished nature of the point $(\tau_0, (1/2)M)$ it seems more sensible to measure time from τ_0 than from zero. Certainly t = 0 is completely arbitrary from the viewpoint of the species, having more to do with whatever external forces (desire, opportunity, availability of funding, and so on) conspired to allow the biologist or census taker to obtain an initial field count than any essential features of the system. Therefore, we consider

$$Q(\tau) := P(\tau_0 + \tau),$$

where τ measures time from τ_0 and hence may be positive or negative. From (3), we have

$$Q(\tau) = \frac{M}{1 + R_0 e^{-k(\tau_0 + \tau)}} = \frac{M}{1 + e^{-k\tau}},$$

since $R_0 e^{-k\tau_0} = 1$. Thus,

$$Q(\tau) - \frac{1}{2}M = \frac{M}{1 + e^{-k\tau}} - \frac{1}{2}M = \frac{1}{2}M\left(\frac{1 - e^{-k\tau}}{1 + e^{-k\tau}}\right) = \frac{1}{2}M\tanh\left(\frac{1}{2}k\tau\right), \quad (8)$$

or

$$P(t) = \frac{1}{2}M\left(1 + \tanh\left(\frac{1}{2}k(t - \tau_0)\right)\right),\tag{9}$$

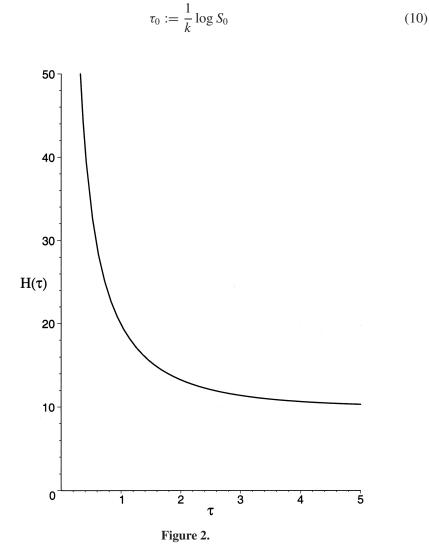
where τ_0 is given by (7). Thus, the mysterious "S-shaped" logistic curve is nothing more than a translate of our old and familiar friend, the hyperbolic tangent.

Addendum

If $0 \le P_0 \le M$, then $\infty \ge R_0 \ge 0$. The boundary cases $P_0 = 0$ and $P_0 = M$ correspond to $R_0 = \infty$, $P(t) \equiv 0$ and $R_0 = 0$, $P(t) \equiv M$, respectively. To complete the analysis of logistic growth, it is necessary to consider what happens when P_0 lies outside the closed interval [0, M], i.e. $R_0 < 0$. The solution (3) is valid for such R_0 , but (9) was predicated on the assumption $R_0 > 0$ in the definition of τ_0 . Putting $S_0 = -R_0$, we have from (3) that

$$P(t) = \frac{M}{1 - S_0 e^{-kt}}, \qquad S_0 > 0.$$

In this case, we define



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so that

$$e^{k\tau_0} = S_0 = \frac{P_0 - M}{P_0}.$$

A calculation analogous to (8) reveals that

$$H(\tau) := P(\tau_0 + \tau) = \frac{1}{2}M\left(1 + \coth\left(\frac{1}{2}k\tau\right)\right),$$

or

$$P(t) = \frac{1}{2}M\left(1 + \coth\left(\frac{1}{2}k(t - \tau_0)\right)\right),$$

where now τ_0 is given by (10).

If $P_0 > M$, then $-1 \le R_0 < 0$, $0 < S_0 = -R_0 \le 1$, and $-\infty < \tau_0 \le 0$. Therefore, for $t \ge 0$ we are on the upper arch of the hyperbolic cotangent, with population decreasing exponentially to M as $t \to \infty$ (Figure 2). In the less biologically meaningful case $P_0 < 0$, we have $-1 \ge R_0 > -\infty$, $1 \le S_0 = -R_0 < \infty$ and $0 \le \tau_0 < \infty$. As t increases from zero to τ_0 , the rightmost portion of the lower arch of the hyperbolic cotangent is traversed, sending the population to minus infinity. The asymptote is then crossed and we skip over to the upper arch, the population reverting to its behaviour in the previous case.

Reference

1. W. Boyce and R. DiPrima, Elementary Differential Equations, 5th ed., Wiley, 1992, p. 54.