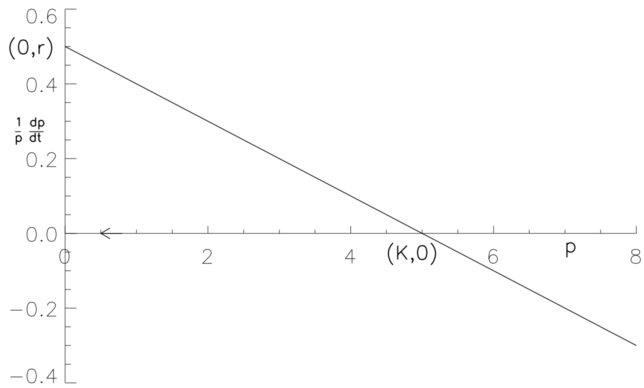
Logistic growth models

We have seen that the constant per capita growth rate model performs poorly as the population grows. This is because individual members compete for finite living space, food, and natural resources in high-density populations. Thus, the population reaches a saturation phase, and nature can carry only so much of it. This saturated population is the carrying capacity K of nature. Consequently, the per capita growth rate is a decreasing function of population size, such that it is almost constant r at low population sizes, zero at the carrying capacity K, and negative at population sizes greater than the carrying capacity.

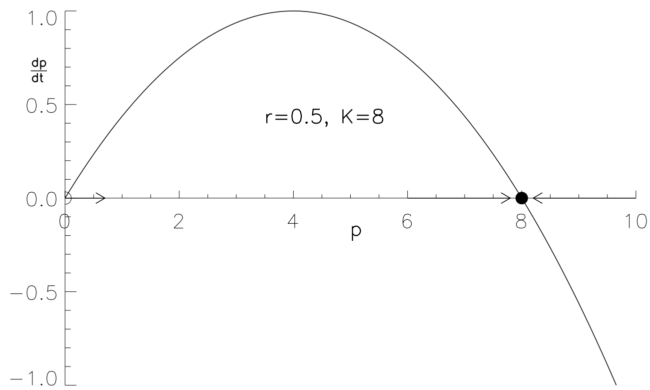


We plot the per capita growth rate against population size. We approximate the per capita growth rate as a straight line passing through $p = 0, \frac{1}{p}\frac{dp}{dt} = r$ and $p = K, \frac{1}{p}\frac{dp}{dt} = 0$:

$$\frac{\frac{1}{p}\frac{dp}{dt}}{r} + \frac{p}{K} = 1 \implies \frac{dp}{dt} = rp\left(1 - \frac{p}{K}\right),$$

subject to initial condition $p(0) = p_0$. This model is known as the Verhulst or logistic model. It has equilibria $p^* = 0$ and $p^* = K$. Note that we can write

$$\frac{dp}{dt} = \frac{rK}{4} - \frac{r}{K}\left(p - \frac{K}{2}\right)^2$$



The plot of growth rate $\frac{dp}{dt}$ against population size p (phase line diagram) gives an inverted parabola with vertex at $\left(\frac{K}{2}, \frac{rK}{4}\right)$ and it passes through $(0,0)$ and $(K,0)$. The phase line diagram shows that any trajectory with initial condition p_0 in $(0,K)$ tends to K as $t \to \infty$. Similarly, any trajectory with initial condition $p_0 > K$ approaches K as $t \to \infty$. Thus, the equilibrium point $p^* = 0$ is unstable and the equilibrium point $p^* = K$ is stable. It is clear that the solution with initial condition $p_0 = 0$ is $p(t) \equiv 0$ whose trajectory remains at $p_0 = 0$ for all time. Similarly, the solution with initial condition $p_0 = K$ is $p(t) \equiv K$ whose trajectory remains at $p_0 = K$ for all time.

From the phase line diagram, it is clear that $\frac{dp}{dt}$ increases in $0 < p < \frac{K}{2}$ and decreases in $p > \frac{K}{2}$. Now

$$\frac{d}{dp}\left(\frac{dp}{dt}\right) = \frac{d^2p}{dt^2}\frac{dp}{dt}$$

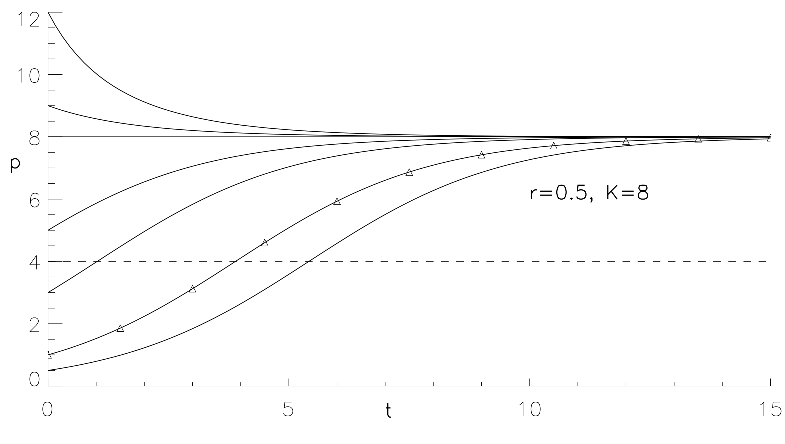
Hence, $\frac{d^2p}{dt^2}\frac{dp}{dt} > 0$ in $0 < p < \frac{K}{2}$ and $\frac{d^2p}{dt^2}\frac{dp}{dt} < 0$ in $p > \frac{K}{2}$. Since $\frac{dp}{dt} > 0$ in $0 < p < K$ and $\frac{dp}{dt} < 0$ in $p > K$, we conclude that

$$\frac{d^2p}{dt^2} \begin{cases} > 0, & p \in \left(0, \frac{K}{2}\right), \\ < 0, & p \in \left(\frac{K}{2}, K\right), \\ > 0, & p \in (K, \infty). \end{cases}$$

This can also be verified directly. Differentiating the growth rate $\frac{dp}{dt}$ with respect to time t, we find that

$$\frac{d^2p}{dt^2} = r\left(1 - \frac{2p}{K}\right)\frac{dp}{dt} = \frac{2r^2}{K^2}p\left(p - \frac{K}{2}\right)(p - K),$$

which verifies the sign of $\frac{d^2p}{dt^2}$ inferred above.



Since $p(t) \equiv 0$ and $p(t) \equiv K$ are trajectories themselves, any trajectory $p(t)$ that starts with an initial condition in $(0,K)$ remains in $(0,K)$ for all time t and approaches the horizontal line $p = K$ as $t \to \infty$. Also, p will increase with time since $\frac{dp}{dt} > 0$ in $0 < p < K$. Since $\frac{d^2p}{dt^2} > 0$ in $0 < p < \frac{K}{2}$, the shape of a trajectory in $0 < p < \frac{K}{2}$ is concave up with p increasing with time (e.g., right branch of parabola $y = x^2$). Since $\frac{d^2p}{dt^2} < 0$ in $\frac{K}{2} < p < K$, the shape of a trajectory in $\frac{K}{2} < p < K$ is concave down with p increasing with time (e.g., left branch of parabola $y = -x^2$). Similarly, the trajectory whose initial point lies in $p > K$ remains in $p > K$ for all time t and approaches the horizontal line $p = K$ as $t \to \infty$. Here, p decreases with time for $p > K$ since $\frac{dp}{dt} < 0$. Further, since $\frac{d^2p}{dt^2} > 0$ in $p > K$, the shape of a trajectory in $p > K$ is concave up with p decreasing with time (e.g., left branch of parabola $y = x^2$). The trajectory whose initial point $p_0 \in \left(0, \frac{K}{2}\right)$ resembles a S-shaped curve (see trajectory marked with triangles), which is also called a logistic curve.

The above conclusions are drawn from the qualitative properties of the logistic model. However, we can easily find its analytical solution. We write

$$\frac{K dp}{p(K-p)} = r\,dt \implies \frac{dp}{p} + \frac{dp}{K-p} = r\,dt \implies \ln \frac{p}{|K-p|} = rt + C$$

Using initial conditions, we find

$$\ln\left(\frac{p}{p_0}\left|\frac{K-p_0}{K-p}\right|\right) = rt$$

Since the solution of an ODE is local, the modulus in the above solution can be removed by continuity. Simplifying we find

$$p(t) = \frac{Kp_0}{p_0 + (K-p_0)\mathrm{e}^{-rt}}$$

When $0 < p_0 < K$, then $p_0 > 0$ and $K - p_0 > 0$ and hence the denominator never becomes zero. Further, the denominator approach p_0 as $t \to \infty$, and hence $p(t) \to K$ as $t \to \infty$ for $0 < p_0 < K$. When $p_0 > K$, then we write the denominator as

$$p_0(1 - \mathrm{e}^{-rt}) + Ke^{-rt} \geq K(1 - \mathrm{e}^{-rt}) + Ke^{-rt} = K$$

In this case too, the denominator is never zero and $p(t) \to K$ as $t \to \infty$ for $p_0 > K$. Combining the results of $0 < p_0 < K$ and $p_0 > K$, we conclude that $p(t) \to K$ as $t \to \infty$ when $p_0 > 0$, which we have also seen using phase line diagram.

Fitting a logistic model to data: Consider the population data shown in the table below:

Time	t_1	t_2	t_3	$\cdots$	t_n
Population	p_1	p_2	p_3	$\cdots$	p_n

We also assume that the time t_is are equispaced. The logistic model is written as

$$\frac{1}{p}\frac{dp}{dt} = r\left(1 - \frac{p}{K}\right)$$

Hence, the ratio of growth rate $\frac{dp}{dt}$ to population p is a linear function of p. Let $h = t_i - t_{i-1}$ for $i = 2, 3, \cdots, n$. Now

$$\frac{p_3 - p_1}{t_3 - t_1} = \frac{p(t_2 + h) - p(t_2 - h)}{2h}$$

Using Taylor series expansion around $t = t_2$, we find

$$\frac{p_3 - p_1}{t_3 - t_1} = \frac{dp(t_2)}{dt} + O(h^2),$$

where $O(h^2)$ implies that the terms are quadratic and higher order. Thus, we approximate $\frac{dp}{dt}$ at time t_2 by $\frac{p_3 - p_1}{t_3 - t_1}$. Using the same approach, we calculate $\frac{dp}{dt}$ at $t_3, t_4, \cdots, t_{n-1}$. Dividing $\frac{dp}{dt}$ by population values p_i leads to the required ratio at t_i for $i = 2, 3, \cdots, n-1$.

Time	t_1	t_2	t_3	$\cdots$	t_{n-1}	t_n
Population	p_1	p_2	p_3	$\cdots$	p_{n-1}	p_n
$\frac{1}{p}\frac{dp}{dt}$		$\frac{p_3-p_1}{p_2(t_3-t_1)}$	$\frac{p_4-p_2}{p_3(t_4-t_2)}$	$\cdots$	$\frac{p_n-p_{n-2}}{p_{n-1}(t_n-t_{n-2})}$	

We plot the ratio along the vertical axis and the corresponding population along the horizontal axis. If the resulting plot is approximately linear, then a logistic model is reasonable. The vertical intercept is r, and the slope must be equal to $-\frac{r}{K}$. Thus, we estimate the approximate value of r and K.

In the above discussion, we have estimated the parameters r and K using only the differential equation. We also know that while solving the logistic model, we arrive at

$$\ln \frac{p}{|K-p|} = rt + C, \qquad (C, \text{arbitrary constant of integration})$$

Assume that the population is below the carrying capacity (i.e., $p < K$). Then, the above becomes

$$\ln \frac{p}{K-p} = rt + C$$

Since this solution assumed the initial time at $t = 0$, we subtract t_1 from the t_is. Using the estimated value of K, we plot $\ln \frac{p}{K-p}$ against time, and we should find a straight line. If the plot does not look straight, then we adjust K, recompute the data and replot until we are satisfied. Now the slope of the line gives a new, improved value of r.