MA 138 – Calculus 2 with Life Science Applications
Handout

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Example 4 (Lotka-Volterra Predator-Prey Model)

- We give an example of a class of differential equations that describes the interaction of two species in a way in which one species (**the predator**) preys on the other species (**the prey**), while the prey lives on a different source of food.
- The population distributions tend to show periodic oscillations.
- We stress upfront that a model involving only two species cannot fully describe the complex relationship among species that actually occur in nature. Nevertheless, the study of simple models is the first step toward an understanding of more complicated phenomena.

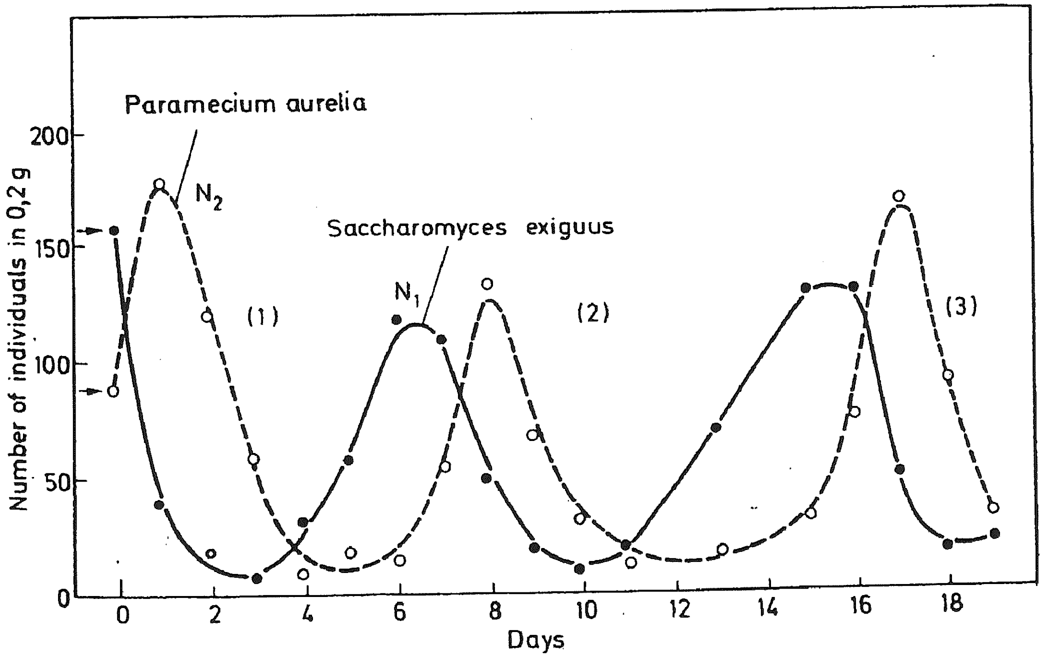
Alfred Lotka (March 2, 1880–December 5, 1949) was a Polish-born mathematician, physical chemist, and statistician, best known for his proposal of the predator-prey model, developed simultaneously but independently of Vito Volterra. The Lotka-Volterra model is still the basis of many models used in the analysis of population dynamics in ecology.

Vito Volterra (May 3, 1860–October 11, 1940) was an Italian mathematician and physicist, known for his contributions to mathematical biology and integral equations.

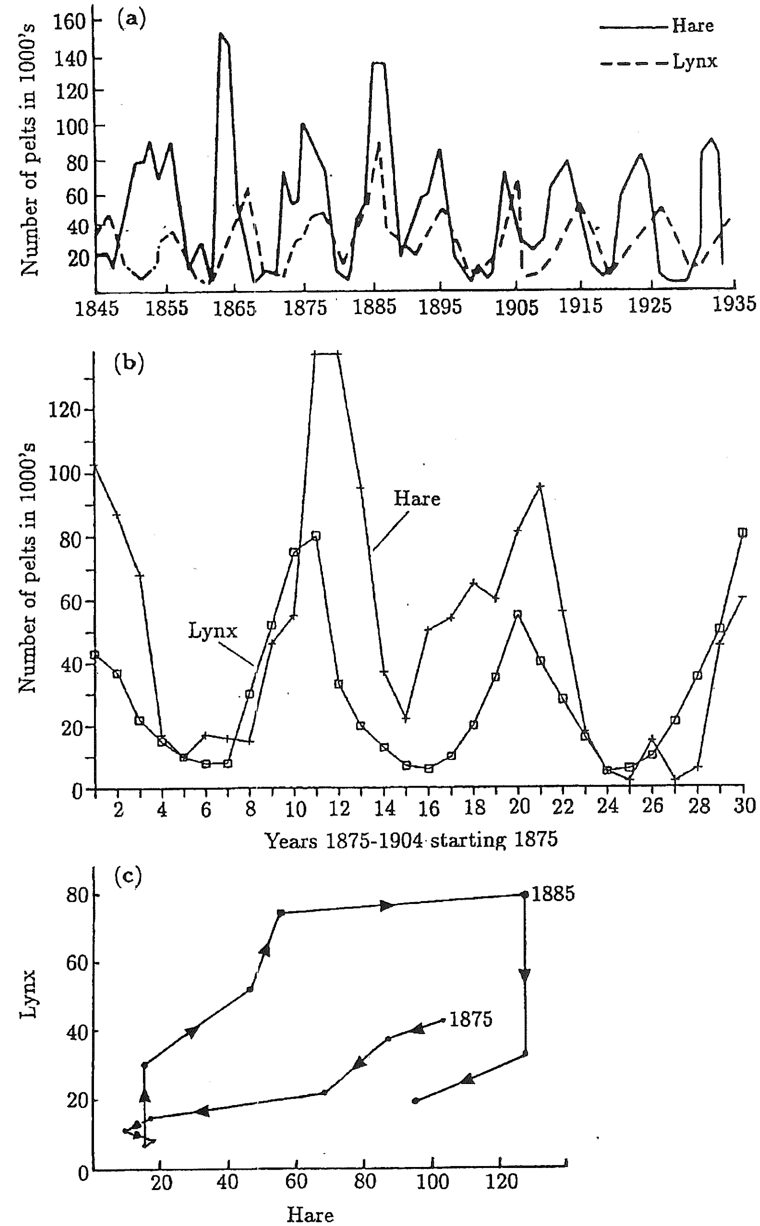
Heuristics

- When the prey population increases in size, the predatory species obtains a larger food base. Hence, with a certain time delay it will also become more numerous.
- As a consequence, the growing pressure for food will reduce the prey population.
- After a while food becomes rare for the predator species so that its propagation is inhibited. The size of the predator population will decline.
- The new phase favors the prey population. Slowly it will grow again, and the pattern in changing population sizes may repeat.
- When conditions remain the same, the process continues in cycles.

The figures below illustrate such cyclical dynamics.



Legend: Fluctuation of population size of *Paramecium aurelia* which feeds upon *Saccharomyces exiguus.*



Legend:

(a) Fluctuations in the number of pelts sold by the Hudson Bay Company.

(b) Detail of the 30-year period starting in 1875.

(c) Phase plane plot of the data in **(b)**.

A (highly simplified) model for the predator-prey interaction can be summarized as follows:

$$\left\{\begin{array}{l}\text{change in}\\ \text{the number}\\ \text{of prey}\end{array}\right\} = \left\{\begin{array}{l}\text{natural}\\ \text{increase}\\ \text{in prey}\end{array}\right\} - \left\{\begin{array}{l}\text{destruction}\\ \text{of prey by}\\ \text{predator}\end{array}\right\}$$

$$\left\{\begin{array}{l}\text{change in}\\ \text{the number}\\ \text{of predator}\end{array}\right\} = \left\{\begin{array}{l}\text{increase in}\\ \text{predator resulting}\\ \text{from devouring prey}\end{array}\right\} - \left\{\begin{array}{l}\text{natural}\\ \text{loss in}\\ \text{predator}\end{array}\right\}$$

We now translate this model into differential equations.

Let $x = x(t)$ be the number of prey individuals and

$y = y(t)$ the number of predator individuals at time instant t.

We assume that x and y are differentiable functions of t.

The **key assumptions** in the Lotka-Volterra model are:

- the birth rate of the prey species is likely to be proportional to x, that is, equal to ax with a certain constant $a > 0$;
- the destruction rate depends on x and on y. The more prey individuals are available, the easier it is to catch them, and the more predator individuals are around, the more stomachs have to be fed. It is reasonable to assume that the destruction rate is proportional to x and to y, that is, equal to bxy with a certain constant $b > 0$.
- the birth rate of the predator population depends on food supply as well as on its present size. We may assume that the birth rate is proportional to x and to y, that is, equal to cxy with a certain constant $c > 0$.
- the death rate of the predator species is likely to be proportional to y, that is, equal to dy with a certain $d > 0$.

Under these simplifying assumptions the differential equations that we obtain are:

$$\frac{dx}{dt} = ax - bxy \qquad \frac{dy}{dt} = cxy - dy.$$

How do we deal these equations?

Because of the interaction between the two populations x (prey) and y (predator), we can view y as a function of x.

As a consequence of the chain rule, we have

$$\underbrace{\frac{dy}{dt} = \frac{dy}{dx} \cdot \frac{dx}{dt}}_{\text{chain rule}} \quad \rightsquigarrow \quad \frac{dy}{dx} = \frac{dy/dt}{dx/dt} \quad \rightsquigarrow \quad \boxed{\frac{dy}{dx} = \frac{(cx-d)y}{x(a-by)}}.$$

Here is a numerical example with $a = 1$, $b = 4$, $c = 2$, and $d = 3$, so that

$$\boxed{\frac{dy}{dx} = \frac{(2x-3)y}{x(1-4y)}.}$$

If we separate the variables this leads to

$$\frac{1-4y}{y}dy = \frac{2x-3}{x}dx \quad \rightsquigarrow \quad \left(\frac{1}{y} - 4\right) dy = \left(2 - \frac{3}{x}\right) dx.$$

After integrating we obtain the solution

$$\ln y - 4y = 2x - 3\ln x + C \quad \rightsquigarrow \quad \ln y + \ln(e^{-4y}) + \ln(x^3) + \ln(e^{-2x}) = C$$

$$\rightsquigarrow \quad \boxed{ye^{-4y}x^3e^{-2x} = \kappa,}$$

where C and $\kappa = e^C$ are constants.

It is worth mentioning that we can write the general solution of the arbitrary Lotka-Volterra equation in the same fashion.

$$\frac{dy}{dx} = \frac{(2x-3)y}{x(1-4y)}$$ separate variables

$$\frac{1-4y}{y}\,dy = \frac{2x-3}{x}\,dx$$ and integrate

$$\int \left(\frac{1}{y} - 4\right) dy = \int \left(2 - 3\cdot\frac{1}{x}\right) dx$$

$$\ln y - 4y = 2x - 3\ln x + C$$

$$\ln y - 4y + 3\ln x - 2x = C$$

$$\ln y + \ln e^{(-4y)} + \ln(x^3) + \ln e^{(-2x)} = C$$

Now use the properties of logarithms and combine

$$\ln\left[y e^{-4y} x^{3} e^{-2x} \right] = C$$

Take exponential of both sides

$$y e^{-4y} x^{3} e^{-2x} = \underbrace{e^{C}}_{\text{call it } K}$$

$$\therefore \quad \boxed{y e^{-4y} x^{3} e^{-2x} = K}$$

unfortunately one cannot solve for y explicitly as a function of x.

In general $$\frac{dy}{dx} = \frac{(cx-d)\,y}{x(a-by)}$$

$$\rightsquigarrow \quad \frac{(a-by)}{y}\,dy = \frac{(cx-d)}{x}\,dx$$

$$\rightsquigarrow \quad \int \left(a\frac{1}{y} - b\right) dy = \int \left(c - d\frac{1}{x}\right) dx$$

$$\rightsquigarrow \quad a \ln y - by = cx - d\ln x + C$$

$$\rightsquigarrow \quad a \ln y - by + d \ln x - cx = C$$

$$\rightarrow \quad \ln(y^a) + \ln\left(e^{(-by)}\right) + \ln(x^d) + \ln\left(e^{(-cx)}\right) = C$$

$$\rightsquigarrow \quad \ln\left[y^a e^{-by} x^d e^{-cx}\right] = C$$

Take now the exponential of both sides and obtain

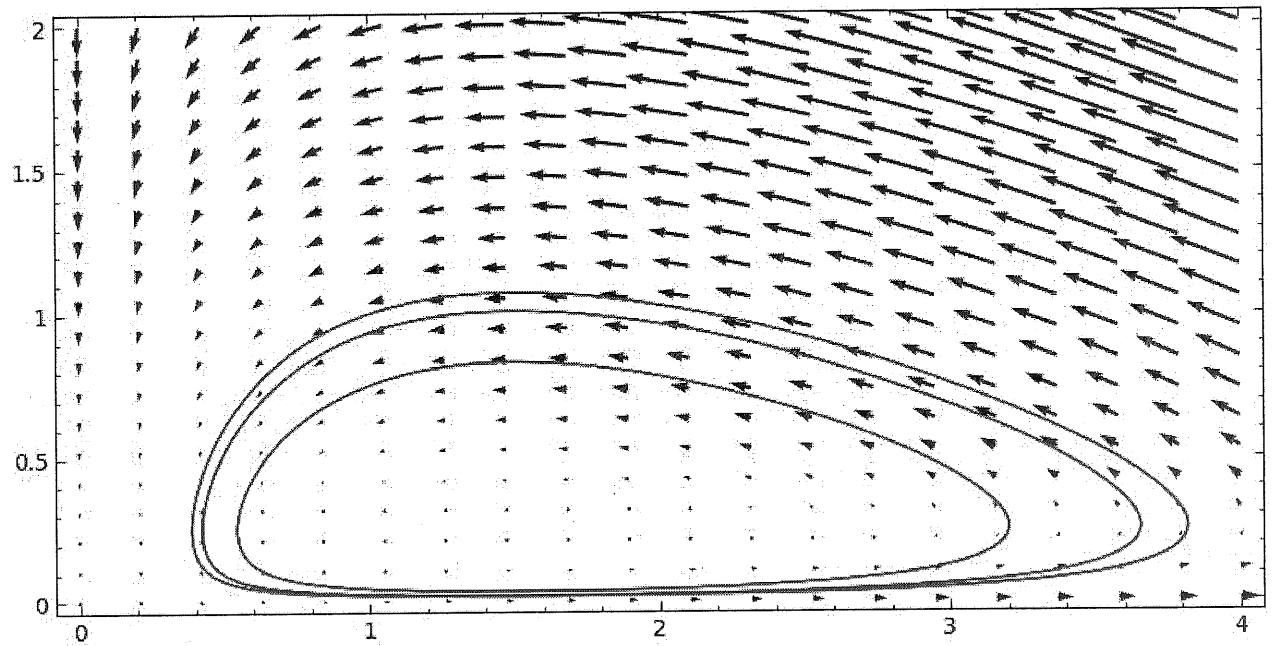
$$y^{a} e^{-by} x^{d} e^{-cx} = \underbrace{e^{C}}_{\text{Constant } K}$$

$$\therefore \quad \boxed{y^{a} e^{-by} x^{d} e^{-cx} = K}$$

which is an implicit equation of y as a function of x.

The graph is given by <u>closed curves</u>.

The direction field of the differential equation $dy/dx = \dfrac{(2x-3)y}{x(1-4y)}$ has been produced with the SAGE commands introduced earlier.



Notice that the trajectories are closed curves. Furthermore, they all seem to evolve around the point $P(3/2, 1/4)$. This is the point where the factors $2x-3$ and $1-4y$ of dy/dt and dx/dt, respectively, are both zero.

This confirms our heuristics that the two populations should exhibit a cyclic dynamic.

Example 5 (Solow's Economic Growth Model von Bertalanffy's Individual Growth Model)

These two models are two different reincarnations of the same differential equation, namely

$$\frac{dy}{dx} = ay^m - by \qquad y(0) = y_0,$$

where a, b, and m are constants.

Robert Solow (born August 23, 1924) is an American economist particularly known for his work on the theory of economic growth that culminated in the exogenous growth model named after him. He was awarded the John Bates Clark Medal (in 1961) and the 1987 Nobel Prize in Economics.

Karl Ludwig von Bertalanffy (September 19, 1901, Atzgersdorf near Vienna–June 12, 1972, Buffalo, New York) was an Austrian-born biologist known as one of the founders of general systems theory (GST). GST is an interdisciplinary practice that describes systems with interacting components, applicable to biology, cybernetics, and other fields. Bertalanffy proposed that the laws of thermodynamics applied to closed systems, but not necessarily to "open systems," such as living things. His mathematical model of an organism's growth over time, published in 1934, is still in use today.

- **Solow's economic growth model:** The capital stock $k = k(t)$ varies over time t, increasing as a result of investments and decreasing as a result of depreciation.

  With these basic assumptions and using a Cobb-Douglass production function, the Solow's growth economic model becomes

$$\frac{dk}{dt} = sk^{\alpha} - \delta k \qquad \text{with} \qquad k(0) = k_0,$$

  where s, α, δ are constants $0 < s,\ \alpha < 1$ and $\delta > 0$.

  The constants s and δ are called the **rate of savings** and the **depreciation rate**, respectively.

- **Von Bertalanffy individual growth model:** The individual growth model published by von Bertalanffy in 1934 is widely used in biological models and exists in a number of permutations.

  In one of its forms it says that the change of body weight W of an individual is given by the difference between the process of building up (anabolism) and breaking down (catabolism)

$$\frac{dW}{dt} = \eta W^{2/3} - \kappa W \qquad \text{with} \qquad W(0) = W_0,$$

  where η and κ are the **constants of anabolism and catabolism**, respectively.

  The exponents $2/3$ and 1 indicate that the latter (anabolism and catabolism) are proportional to some powers of the body weight W.

Solving: $dy/dx = ay^m - by \qquad y(0) = y_0$

Consider the differential equation given earlier

$$\boxed{\frac{dy}{dx} = a\,y^m - b\,y} \qquad \rightsquigarrow \qquad \frac{dy}{dx} = y^m(a - b\,y^{1-m}).$$

This suggests the use of the substitution $u = y^{1-m}$. The chain rule says

$$\frac{du}{dx} = \frac{du}{dy}\cdot\frac{dy}{dx} \quad \rightsquigarrow \quad \frac{du}{dx} = (1-m)\,y^{[(1-m)-1]}\,\frac{dy}{dx} \quad \rightsquigarrow \quad \frac{1}{1-m}\,y^m\,\frac{du}{dx} = \frac{dy}{dx}.$$

If we now substitute the latter expression into our original differential equation we get the separable differential equation below

$$\frac{du}{dx} = (1-m)\,(a - b\,u).$$

Separate the variables, multiply both sides by $-b$, and integrate. We get

$$\frac{b}{b\,u-a}\,du = -(1-m)\,b\,dx \quad \rightsquigarrow \quad \ln(b\,u-a) = -(1-m)\,b\,x + C$$

where C is a constant.

After additional manipulations and substituting back y^{1-m} in place of u:

$$y = \left[\frac{a}{b} + D\cdot e^{-(1-m)\,b\,x}\right]^{1/(1-m)},$$

where $D = e^C/b$. The initial condition $y(0) = y_0$ gives us: $D = y_0^{1-m} - \dfrac{a}{b}$.

Thus the solution of our initial value problem is

$$\boxed{y = \left[\frac{a}{b} - \left(\frac{a}{b} - y_0^{1-m}\right)\cdot e^{-(1-m)\,b\,x}\right]^{1/(1-m)}.}$$

Notice that $y_\infty = \lim_{x\to\infty} y = \left[\dfrac{a}{b}\right]^{1/(1-m)}.$

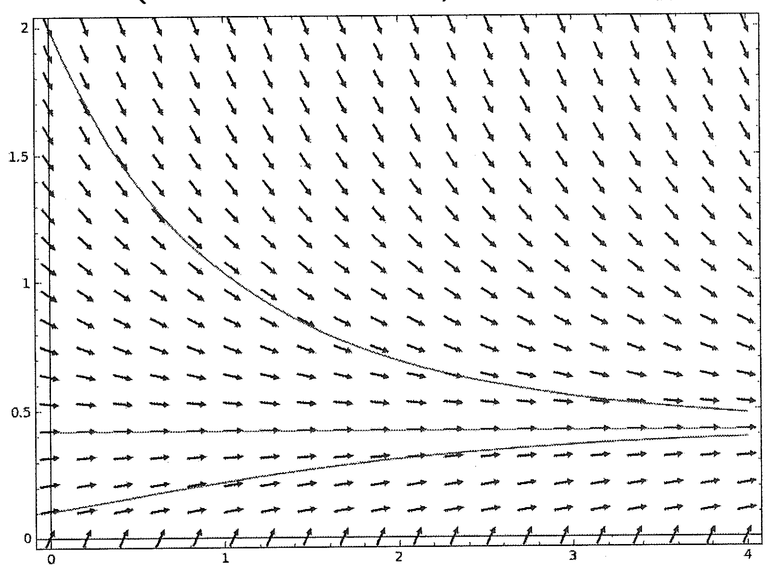
When $m = 2/3$

Our model with initial condition $y(0) = y_0$ and asymptotic value y_∞ is

$$\frac{dy}{dx} = a\,y^{2/3} - b\,y \quad \rightsquigarrow \quad y = \left[\frac{a}{b} - \left(\frac{a}{b} - y_0^{1/3}\right) \cdot e^{-bx/3}\right]^3 \qquad y_\infty = \left[\frac{a}{b}\right]^3.$$

Here is an example with $a = 1.5$, $b = 2$, and $m = 2/3$, so that

$$\frac{dy}{dx} = 1.5\,y^{2/3} - 2\,y \qquad \rightsquigarrow \qquad y = \left[0.75 - \left(0.75 - \sqrt[3]{y_0}\right) e^{-2/3x}\right]^3.$$



The direction field of the given DE is on the right-hand side.

Notice that as $x \longrightarrow \infty$ all the solutions approach the value

$$y_\infty = (1.5/2)^3 \approx 0.422.$$

Example 6 (Tumor Growth)

A tumor can be modeled as a spherical collection of cells and it acquires resources for growth only through its surface area. All cells in a tumor are also subject to a constant per capita death rate. The dynamics of tumor mass M (in grams) might therefore be modeled as

$$\frac{dM}{dt} = \eta M^{2/3} - \kappa M \qquad M(0) = M_0$$

where η and κ are positive constants. The first term represents tumor growth via nutrients entering through the surface. The second term represents a constant per capita death rate.

Assuming tumor mass is proportional to its volume, the diameter of the tumor is related to its mass as $D = aM^{1/3}$, where $a > 0$. Derive a differential equation for D and show that it has the form of the von Bertalanffy restricted growth equation (that we saw in a previous lecture).

$$\frac{dM}{dt} = \eta M^{2/3} - kM \qquad M(0) = M_0$$

It is suggested that $\boxed{D = a M^{1/3}}$ (*) where $a > 0$

$$\frac{dD}{dt} = a \frac{d}{dt}(M^{1/3}) = \text{by the chain rule} = a \frac{d}{dM}(M^{1/3}) \frac{dM}{dt}$$

$$= a \frac{1}{3} M^{1/3 - 1} \frac{dM}{dt} = \frac{a}{3} M^{-2/3} \frac{dM}{dt}$$

or $$\boxed{\frac{dM}{dt} = \frac{3}{a} M^{2/3} \frac{dD}{dt}}$$

(*) This makes sense because the volume of a sphere $V_S = 4/3 \pi R^3$. But $2R = D$ so $V_S = \frac{4}{3}\pi \left(\frac{D}{2}\right)^3 = \frac{4}{3}\pi \frac{D^3}{8}$ $\therefore$ $V_S = \frac{\pi}{6} D^3$. The <u>mass</u> will be <u>proportional to the volume</u> (if the cell is homogeneous).

Notice also that $D = a M^{1/3}$ so if we square it we get: $D^2 = a^2 M^{2/3}$ so

$$\boxed{M^{2/3} = \frac{1}{a^2} D^2}$$

Moreover $D^3 = a^3 (M^{1/3})^3 \Longrightarrow$

$$\boxed{M = \frac{1}{a^3} D^3}$$

Thus:

$$\frac{dM}{dt} = \eta M^{2/3} - k M$$

becomes:

$$\frac{3}{a} \underbrace{M^{2/3}}_{\frac{1}{a^2} D^2} \frac{dD}{dt} = \eta \left(\frac{1}{a^2} D^2 \right) - k \left(\frac{1}{a^3} D^3 \right)$$

$$\boxed{\frac{3}{a^3} D^2 \frac{dD}{dt} = \frac{\eta}{a^2} D^2 - \frac{k}{a^3} D^3}$$

Simplify D^2/a^2 throughout and we obtain:

$$\frac{3}{a}\frac{dD}{dt} = \eta - \frac{k}{a}D$$

or

$$\frac{dD}{dt} = \frac{a\eta}{3} - \frac{k}{3}D$$

which is a simple Von Bertalanffy DE.

Separate variables

$$\frac{1}{\frac{a\eta}{3} - \frac{k}{3}D}\, dD = 1 \cdot dt$$

Multiply both sides by $-k/3$

$$\int \frac{-k/3}{\frac{a}{3}\eta - \frac{k}{3}D} \cdot dD = \int -\frac{k}{3}\, dt$$

$$\therefore \quad \ln\left(\frac{a}{3}\eta - \frac{k}{3}D\right) = -\frac{k}{3}t + C$$

Take exponentials of both sides

$$\boxed{\frac{a}{3}\eta - \frac{k}{3}D = A \cdot e^{-\frac{k}{3}t}} \qquad A = e^{C}$$

Since $M(0) = M_0$ and $D = a M^{1/3}$

we have $\boxed{D(0) = a\, M_0^{1/3}}$

Thus $\quad \frac{a}{3}\eta - \frac{k}{3} a M_0^{1/3} = A \cdot \underbrace{e^{0}}_{=1}$

$\therefore \quad A = \frac{a\eta}{3} - \frac{k}{3} a M_0^{1/3}$

Hence $\quad \frac{a}{3}\eta - \frac{k}{3} D = \left(\frac{a\eta}{3} - \frac{ka}{3} M_0^{1/3} \right) e^{-k/3\, t}$

Simplify $1/3$ throughout:

$$kD = a\eta - \left(a\eta - k a M_0^{1/3} \right) e^{-k/3\, t}$$

$$\therefore \boxed{D = \frac{a}{k}\eta - \left(\frac{a}{k}\eta - a M_0^{1/3} \right) e^{-k/3\, t}} \quad ||_{1/2}$$

Note that $\lim_{t \to \infty} D(t) = \frac{a}{k}\eta = D_\infty$

Example 7 (Gompertz Model of Tumor Growth)

Another model of tumor growth is given by the Gompertz model. This tumor growth model assumes that the per volume growth rate of the tumor declines as the tumor volume gets larger according to the equation

$$\frac{dV}{dt} = aV(\ln b - \ln V)$$

where a and b are positive constants.

Show that the solution of this DE with initial tumor volume $V(0) = V_0$ is

$$V(t) = b \cdot \exp\left[-\ln\left(\frac{b}{V_0}\right)e^{-at}\right].$$

Observe that $\lim_{t \longrightarrow \infty} V(t) = b$.

Note:

This model is sometimes used to study the growth of a population for which the per capita growth rate is density dependent.

$$\frac{dV}{dt} = aV(\ln b - \ln V)$$

Separate the variables (a and b are constants)

$$\frac{1}{V} \cdot \frac{1}{(\ln b - \ln V)} \, dV = a \, dt$$

Notice that $\frac{d}{dt}(\ln b - \ln V) = -\frac{1}{V}$. Thus if we multiply both sides by "−1" we have

$$\underbrace{\int -\frac{1}{V} \cdot \frac{1}{(\ln b - \ln V)} \, dV}_{\ln[\ln(b) - \ln V]} = \underbrace{\int -a \, dt}_{-at + C}$$

∴ if $\ln[\ln(b) - \ln(V)] = -at + C$

Take exponentials of both sides and we obtain

$$\ln(b) - \ln(V) = A \cdot e^{-at} \quad \text{where } A = e^{C}$$

Now use the initial condition to determine A.

$V(0) = V_0$. Thus:

$$\ln(b) - \ln(V_0) = A \cdot \underbrace{e^{0}}_{1} \quad \therefore \quad A = \ln\left(\frac{b}{V_0}\right)$$

using the properties of logarithms.

Hence:

$$\ln(V) = \ln b - \underbrace{\ln\left(\frac{b}{V_0}\right)}_{A} \cdot e^{-at}$$

Now take again the exponential of both sides

$$V(t) = e^{\ln b - \ln(b/V_0)e^{-at}} = b \cdot e^{-\ln(b/V_0)e^{-at}}$$

↑ use the usual properties of exponentials