

Modelling Population Growth

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Introduction

Understanding populations and their dynamics is a crucial element in biology. Its importance is highlighted by the fact that a completely self-sufficient scientific field - demography - was developed to that purpose. In *Analytical Theory of Biological Populations*, Alfred J. Lotka (1880-1949), one of the founding fathers of demography, devises the term *general demology* as a new branch of biological science 'concerned with the analytical study of aggregations formed by populations of diverse biological organisms' (Lotka, 1998, p.3).

In this work divided into five sections, I aim to explore the mathematical methods introduced by Lotka and his contemporaries and reach an understanding of population changes with stress on human population growth. In the first section, I provide motivation for predicting quantitative behaviour of human populations. The second section involves a brief formulation of the issue as observed in reality, i.e. the biological point of view. The transition from the real to the abstract is described in the third section, in which I gradually develop three models beginning with the simplest assumptions and then moving to more complex settings. The fourth section is concerned with additional remarks on the mathematics of the models. In the final section, I evaluate the models with focus on potential discrepancies between the mathematical solution and the real-world situation. Full step-by-step solutions to the main equations are presented in the Appendix.

Motivation

The importance of predicting the correct rate of human population growth becomes clear at a brief glance towards the recent history of mankind. I consider fear of overpopulation to be a dangerous phenomenon to be avoided, as it led to multiple inhuman policies throughout the 20th century such as eugenics in the USA and the infamous one-child policy in China (Weiss, 2019).

In 1798, Thomas Malthus published *An Essay on the Principle of Population*, in which he argues that the number of people on Earth is growing at a quicker rate than the amount of resources and the expected result in future is famine and starvation (Malthus, 1998). This essay was the first to spark fear of overpopulation and even today aids many arguments in favour of population planning. I discuss the model that Malthus used for his predictions later in the text.

The Population Bomb, a bestseller published by Paul Ehrlich in 1968, is another example of a panic-invoking work concerning rapid population growth. The political consequences of this more recent publication were also dire (Mann, 2018), yet we now see that the famine predicted by Ehrlich has never come.

In the 21st century, it is still common to see commentators worry about overpopulation and consequential starvation (Connor, 2006; Whiting, 2018). With climate change on the rise and the indisputable role of humanity in causing it, we can see how population growth can be harmful to the environment by the simple logic of 'more people create more emissions and more waste' (Leblanc, 2018). During the completion of this work, Senator Bernie Sanders, one of the leading figures of the Democratic Party in the US and a potential presidential candidate, argued that population control should play a role in solving the climate crisis (BBC, 2019). However, it is necessary to work with carefully crafted predictions which keep us reasonable and pragmatic. Whenever one talks about the possible consequences of population growth, and it does not matter whether one is an optimist or a pessimist, it is crucial that their reasoning is based on realistic models and correct data.

The real-world formulation of the problem

The object under study is a population, defined as 'a set of organisms of the same species living in a particular place and time' (Haefner, 2005, p. 272), and its evolution. The task is to determine its size at any time given its size at the initial time. Another important piece of information is a measure of increase or decrease in the population in the beginning of the studied period. The population can have additional properties influencing the evolution, some of which are introduced later in the text. For clarity and brevity, I study only isolated populations (i.e. no emigration or immigration is allowed). It is also assumed that the population is settled within a certain territory and changes occur only in time, not in space.

The task

Consider an isolated population. Reproduction is a continuous process. Find a suitable way to predict the population growth or decline and thus estimate the population size at any time in the future.

There is an essential distinction that needs to be considered when building almost any mathematical model. The issue concerns the passage of time. Does one wish to treat time as a step-by-step process, or rather as a continuous entity? That is, should one use a discrete or a continuous model? In our case, the former is to consider each generation as if detached from the previous one, while the latter allows for continuous reproduction. To provide an example, when considering a bacteria population, one usually assumes a certain rule, e.g. 'every hour, the number of bacteria doubles'. This problem is best tackled by a discrete model, since one calculates with a constant time step between each generation. However, if it is necessary to make more complex assumptions, one is forced to devise a continuous model, which usually involves differential equations (Haefner, 2015). This is the case for all models presented in this text.

Building the models

I begin with basic definitions that provide a translation from the biological to the mathematical realm.

As convention requires, time (measured in years) shall be denoted by t . A population of a single species is a single-valued time-dependent function denoted by $N(t)$. The initial population is the value $N(t)$, commonly abbreviated to N_0 . An annual change in population is $\frac{\Delta N}{\Delta t}$.

As noted above, populations studied in this work are assumed to be isolated. It immediately follows that

$$\frac{\Delta N}{\Delta t} = B - D \quad (1),$$

where B and D denote respectively the number of births and the number of deaths in the current year. This is the most general discrete formulation of the equations to be studied. A continuous version of the general formulation is

$$\frac{dN}{dt} = f(N) \quad (2),$$

where $f(N)$ is a general function and its particular form is to be derived from biological data and assumptions.

Now, with the necessary definitions, the problem transforms into a differential equation, which is to be solved given certain initial conditions. Depending on assumptions for the function $f(N)$, we obtain the following equations, which comprise our models.

Model 1: Malthusian growth

Assuming that the annual increase in population is constant, we deduce from (1) that the annual increase per capita, denoted by r and obtained statistically, is the value

$$r = \frac{\Delta N}{N\Delta t} = \frac{B - D}{N}.$$

It follows that

$$\frac{\Delta N}{\Delta t} = rN \quad (3a).$$

Now, if the magnitude of r remains within certain bounds, which is the case for most human populations, we can transfer from the discrete to the continuous and obtain the equation

$$\frac{dN}{dt} = rN \quad (3b),$$

with the solution

$$N(t) = N_0 e^{rt} \quad (\text{Malthusian growth}).$$

Depending on the sign of r , the result is either exponential growth, or exponential decline. We are often interested in the behaviour of the function at the limit $t \rightarrow \infty$. In this case, if r is positive, the function diverges to positive infinity, a fairly unrealistic result. If r is negative, the limit is equal to zero, meaning the resulting state is extinction of the population.

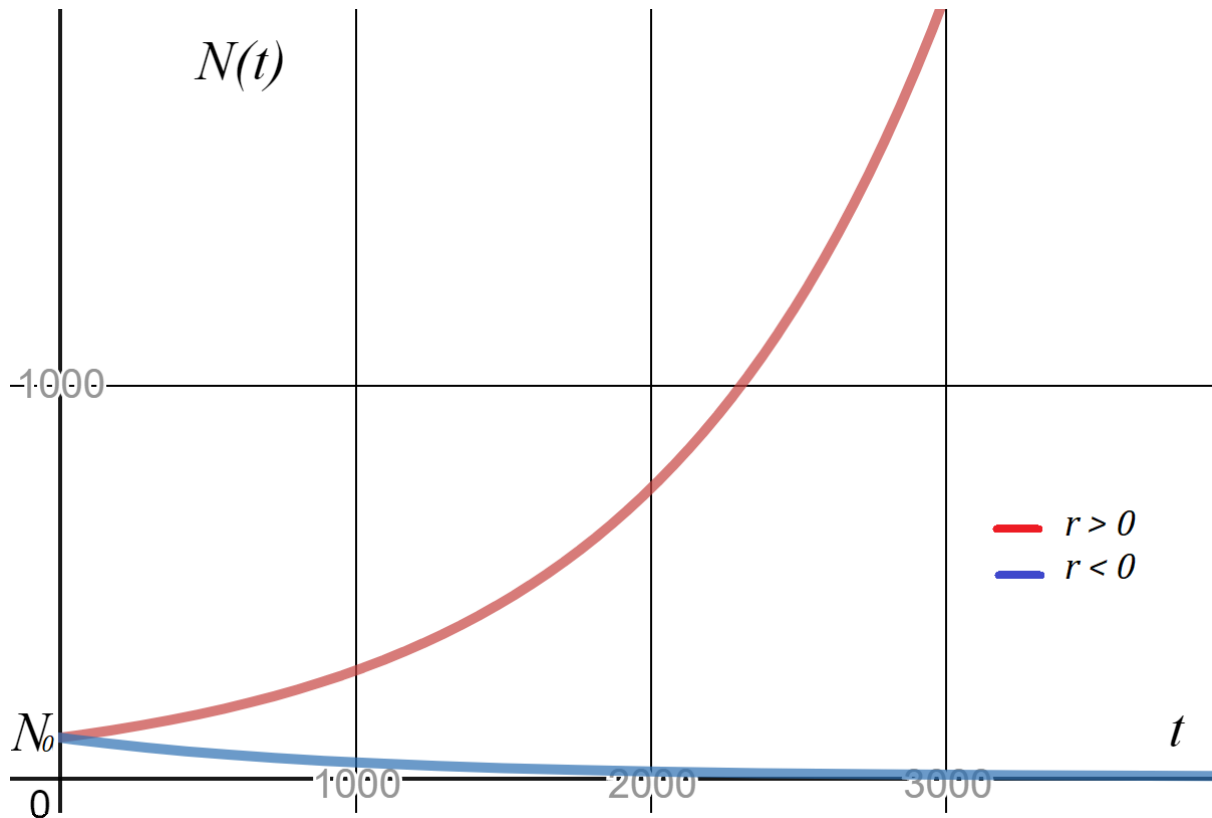


Figure 1: Malthusian law with $N_0 = 100$. Figures 1, 2 & 4 were created using www.desmos.com.

Model 2: logistic growth

The second model differs from the first one in that we do not assume constant annual increase in the population. Vaguely put, we assume instead that the population growth gradually slows down as the population gets larger. This assumption has a reasonable biological basis: with larger populations, resources tend to get exhausted more quickly, resulting in population decline. Even though this is the case for animals rather than humans, the following model fits data from the 20th century USA, so it is relevant to human populations, too (Lotka, 1998, p. 95). Here, it is necessary to introduce a new variable C . It denotes the *carrying capacity* of an environment, which is 'the average population density or population size of a species below which its numbers tend to increase and above which its numbers tend to decrease' (Britannica, 2007). In our case, C is considered to be a size.

To convert the vague assumption into a concrete mathematical expression, we add a quadratic term involving C to the function $f(N)$, which results in

$$f(N) = rN \left(1 - \frac{N}{C} \right).$$

The expression $1 - \frac{N}{C}$ is positive when $N < C$ and negative when $N > C$ (and so is the value of $f(N)$ for positive r). This is a mathematical translation of the intuition 'growth until reaching C , then decline'. We have the equation

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{C}\right) \quad (4),$$

which yields the solution

$$N(t) = \frac{N_0 C}{N_0 + (C - N_0)e^{-rt}} \quad (\text{logistic growth}).$$

In contrast with the Malthusian model, this solution produces *stable states* for positive values of r . A stable state is understood as a positive real value of $N(t)$ as $t \rightarrow \infty$, which means the population is capable of surviving at current conditions. Unsurprisingly, the limit is equal to the carrying capacity of the population. For negative r , the limit again equals zero. A special case is the initial condition $C = N_0$, which results in a stable state at the carrying capacity for any r . Substituting into the logistic growth function shows that the population is not dependent on time in this case – in other words, it is constant.

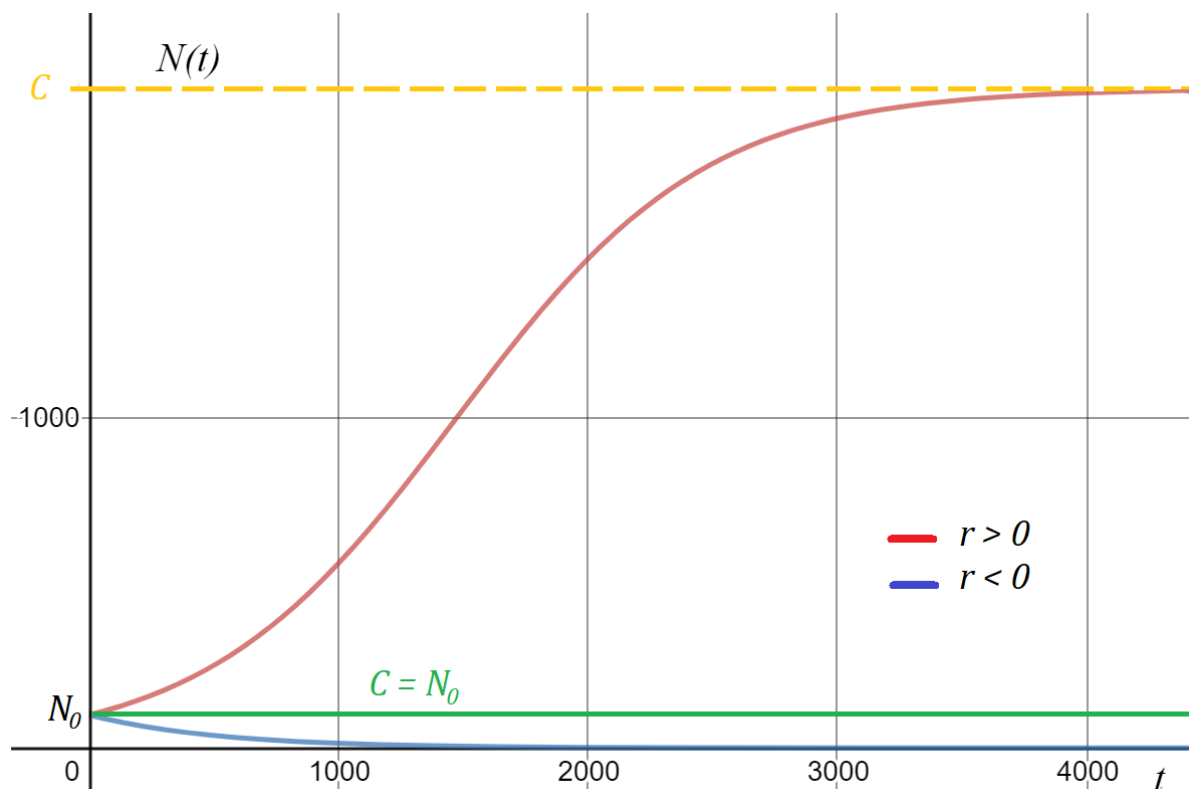


Figure 2: Logistic growth with $N_0 = 100$ and $C = 2000$. Includes the special case (green) with $C = N_0 = 100$.

Model 3: Allee effect

In the last model, we assume a certain population size to be optimal for reproduction. Again, this requires a new variable. This optimal population shall be denoted by A . The reproduction rate increases until the population reaches A ; then reproduction slows down. We proceed by adding a term involving A to the function $f(N)$. As previously, the term should somehow capture the critical threshold, which is A in this case. One of the possible and simplest variations is $N - A$ (negative when $N < A$, positive when $N > A$). For scaling, we divide by C . Hence, we get

$$f(N) = rN \left(1 - \frac{N}{C}\right) \frac{N - A}{C}.$$

Therefore

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{C}\right) \frac{N - A}{C} \quad (5),$$

a simple version of the *Allee effect*.

The solution to the equation is fairly complicated and beyond the scope of this work.¹ Moreover, it is dependent on the three variables r , A and C and it is not sensible to present it in the wide scope that can be reached by adjusting the constants. Instead, it is possible to infer a few observations of the qualitative behaviour of the population.

We distinguish between *strong* and *weak* Allee effects. A strong Allee effect occurs when the initial reproduction rate r is negative, while a weak Allee effect occurs when r is positive. The weak Allee effects behave in a way similar to the logistic growth. In the strong version, the behaviour of the population depends on initial conditions. There are two possible outcomes depending on whether the initial population is large enough, i.e. whether it holds that $N_0 < A$, or $N_0 > A$ (see Figure 3). In the former case, the population reaches extinction, while in the latter case, a delayed logistic growth occurs and the population settles at the carrying capacity (Drake & Kramer, 2011).

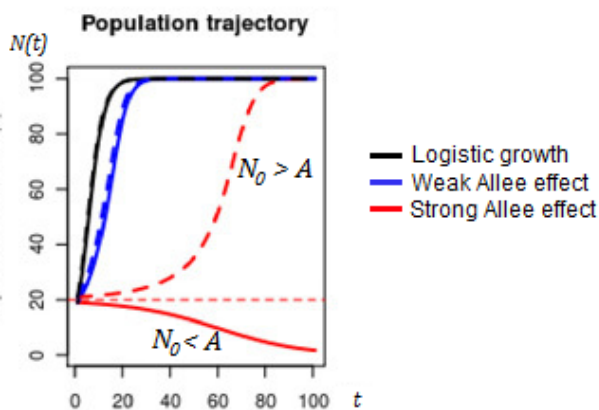


Figure 3: Allee effects compared to logistic growth. Adapted from Drake & Kramer (2011).

¹ In fact, none of the consulted literature presents an explicit solution to the equation.

Some additional mathematical remarks on the models

Apart from the biological arguments for using the equations above, there is a reasonable mathematical justification for the consequential steps leading from Model 1 to Model 3. If we assume that the general function $f(N)$ is sufficiently smooth, it follows that there is a Taylor series expansion for $f(N)$. As we progress through the models, we take more terms of the expansion at every step.

$$\text{Assume } f(N) = a_0 + a_1N + a_2N^2 + a_3N^3 + \dots$$

By *Axiom of Parenthood* (every organism must have parents, there is no spontaneous generation of organisms), we have $\frac{dN}{dt}(0) = f(0) = 0$, which yields $a_0 = 0$ (Edelstein-Keshet, 2005, p. 214). Hence the simplest 'piece' of the Taylor expansion to be considered is the linear term a_1N , which results in equation (1) with $a_1 = r$. In equation (2), we have two terms coming from the Taylor series of $f(N)$, namely $a_1N + a_2N^2$ with $a_1 = r$ and $a_2 = -\frac{r}{c}$. The Allee effect equation makes use of three terms up to cubic.

Since $a_0 = 0$, we can rewrite $f(N) = N(a_1 + a_2N + a_3N^2 + \dots) = Ng(N)$. The function $g(N)$ is called the *intrinsic growth rate* of the population and its behaviour is the most straightforward tool for understanding the relation between the real and the abstract. In Model 1, we see that $g(N) = r$, a constant, meaning that the reproduction rate is the same at all times, which is exactly the assumption we made. Adding a second term in Model 2 changes $g(N)$ to a linear decreasing function, which agrees with the assumption that the reproduction slows down as population increases. In Model 3, $g(N)$ is a quadratic function with a maximum in A . This fits the assumption that the reproduction rate increases until the population density reaches a certain point corresponding to A and then it declines.

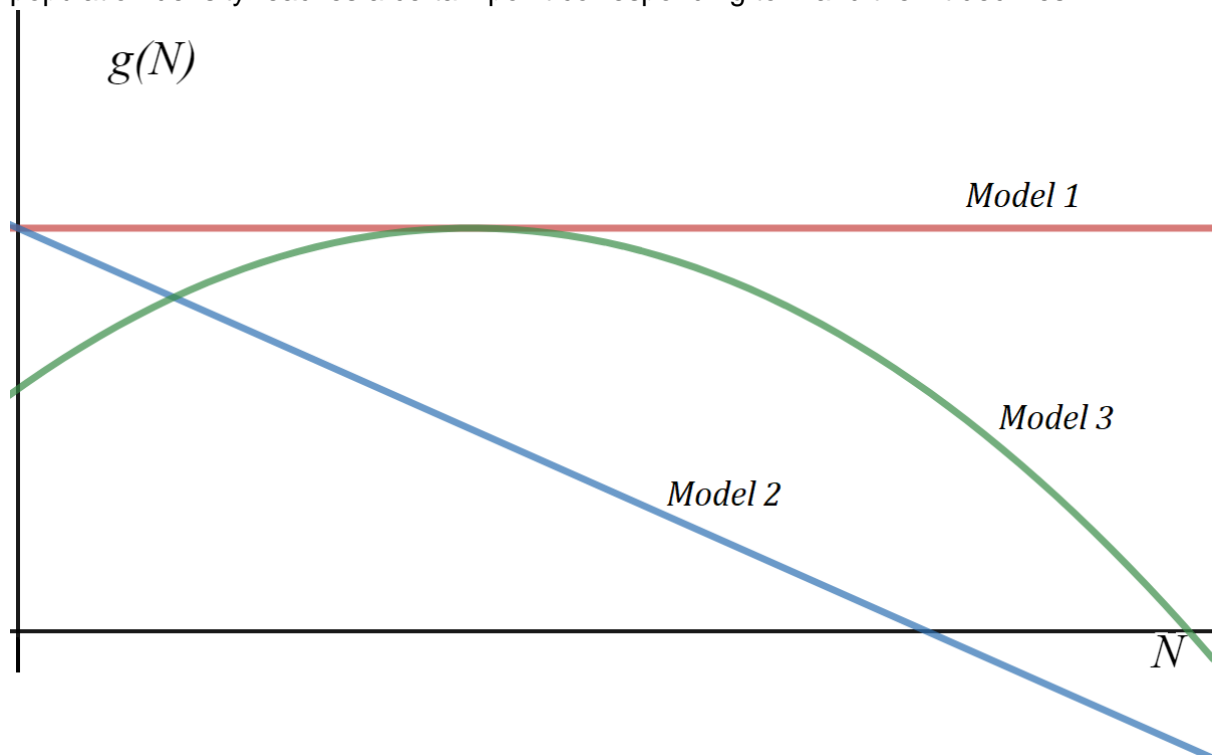


Figure 4: Sketches of the intrinsic growth rate function $g(N)$ for each model.

From the analysis above, it is clear that one could produce a large variety of models by making use of the function $g(N)$. Development of reproduction rate in a population can be converted to function behaviour and with a new function one obtains a new differential equation, i.e. a new model. An example of this would be the *Gompertz law*, which assumes $g(N)$ to be a decreasing logarithmic function and finds use in oncology when modeling growth of tumors (Edelstein-Keshet, 2005, p. 217).

Discussion

The field of population dynamics offers a lot more than the three introductory equations presented in this work. Populations are complicated and have a tendency to be influenced by far more factors than are captured by the models. For example, a crucial assumption of this work is that studied populations are isolated. Without this assumption, the elementary equation $\frac{\Delta N}{\Delta t} = B - D$ needs to be modified to include immigration and emigration.

Furthermore, the behaviour of populations is affected by other species and environment. Human populations are influenced by complex social interactions. Biological evolution of a population is a stochastic process and thus any deterministic model that we create will not be able to completely capture its behaviour.² In simpler words, the world of mathematics is predictable, while the real world is not. As the anecdote popular among statisticians and attributed to George E. P. Box says: 'All models are wrong, but some are useful.' (Barroso, 2018).

Moreover, ecosystems often display chaotic behaviour, which albeit being deterministic is a feature our models are not capable of capturing. Chaos, a sensitive dependence to initial conditions exhibited by a dynamical system, causes a serious complication in our ability to understand and predict biological processes in general (Bishop, 2017).

It is possible to tackle the issue in an alternative way. Instead of using a deterministic equation based on simple biological assumptions, one can resort to the arsenal of stochastic methods provided by the field of statistics. With human populations, there is usually a great amount of data to extrapolate from. Statistical methods might provide a higher level of practicality, especially when making predictions.

Nevertheless, the models presented in this text provide a piecewise understanding of intrinsic populations' behaviour. Coming back to Alfred J. Lotka, it is the inherent dynamic qualities of a general population that theorists should be interested in, as opposed to approximation-based predictions. What this work hopefully managed is to capture and explain some of those qualities expressed in the language of mathematics.

² A deterministic process is completely determined by its initial state and hence predictable once one has enough information. This is the case for our models – their solutions are determined by the equations and initial conditions. On the other hand, a stochastic process admits probabilistic factors and it is therefore impossible to predict its evolution in the future with absolute certainty.

Appendix: solutions to the central equations

Model 1

We solve the equation

$$\frac{dN}{dt} = rN \quad (3b).$$

We can rewrite (3b) as

$$\frac{dN}{N} = r dt.$$

Integrating both sides, we get

$$\ln N = rt + K,$$

where K denotes the integration constant. Applying exponential operator to the both sides of the equation yields

$$N(t) = e^{rt+K} = K'e^{rt},$$

where K' denotes a constant to be expressed in terms of the initial condition N_0 . Substituting $t = 0$ into the equation, we have $K' = N(0)$, so the final solution is

$$N(t) = N_0 e^{rt} \quad (\text{Malthusian growth}).$$

Model 2

We solve

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{C}\right) \quad (4).$$

Rewriting (4) as

$$\frac{dN}{N \left(1 - \frac{N}{C}\right)} = r dt,$$

we can integrate both sides. To integrate the left-hand side, we use partial fraction expansion, obtaining

$$\int \left(\frac{1}{N} + \frac{\frac{1}{C}}{1 - \frac{N}{C}} \right) dN = \int \left(\frac{1}{N} + \frac{1}{C - N} \right) dN = \int r dt.$$

After integration, we have

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

Hence,

$$\frac{N}{C - N} = K'e^{rt} \quad (A).$$

To find an explicit expression for $N(t)$, we rearrange the terms in the equation and get

$$N(t) = \frac{CK'e^{rt}}{1 + K'e^{rt}}.$$

To express K' in terms of N_0 and C , we substitute $t = 0$ into equation (A) and obtain

$$K' = \frac{N_0}{C - N_0}.$$

Therefore

$$N(t) = \frac{C \frac{N_0}{C - N_0} e^{rt}}{1 + \frac{N_0}{C - N_0} e^{rt}} = \frac{N_0 C e^{rt}}{C - N_0 + N_0 e^{rt}}.$$

Multiplying both the numerator and the denominator by e^{-rt} , we reach the final form of the solution, which is

$$N(t) = \frac{N_0 C}{N_0 + (C - N_0)e^{-rt}} \quad (\text{logistic growth}).$$

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