Research on Population Behavior

Dengyuhan Dai

March 20, 2026

Abstract

This article will mainly discuss the models for simulating the evolution of animal populations through ordinary differential equations, and will also provide examples of the simulation of real data using some of these models. Through the study of these models, this article will also propose some possible directions for model improvement to make them more in line with real animal evolution.

Contents

1 Introduction

1.1 Motivation

From ancient times to the present, the evolution of populations has always been a subject of our concern. This not only pertains to the development of human beings themselves, but also closely relates to the populations we raise and the species we hunt. Nowadays, with more advanced mathematical knowledge, we can conduct a deeper study on this topic. This is also my primary motivation: I want to use my professional knowledge to understand this topic, which is closely related to our lives, better.

1.2 Basic concepts

To facilitate the discussion of these models, we first introduce several common mathematical definitions together with their biological interpretations.

Remark 1.1 (Fixed Point). *In population models, a fixed point means that the population size will* ***remain*** *at this position. This can have various meanings, such as the birth rate and death rate being equal, the population size being constantly equal to 0, or the population size reaching a certain upper limit.*

Remark 1.2 (Stability). *The* stability *of a fixed point represents whether a population level is robust under small environmental effects or not in biology meaning.*

Definition 1.1 (Inflection Point). *An* inflection point *is a point where the solution curve changes concavity. For a function $x(t)$, this occurs at a point t^* such that*

$$\frac{d^2x}{dt^2}\bigg|_{t=t^*} = 0,$$

with a change in sign of the second derivative. In population models, this typically represents the transition from accelerating growth to decelerating growth.

Definition 1.2 (Root Mean Square Error (RMSE)[4]). *Let $y_1, y_2, \ldots, y_n$ be observed values and $\hat{y}_1, \hat{y}_2, \ldots, \hat{y}_n$ be the corresponding predicted values. The root mean square error (RMSE) is defined as*

$$\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}.$$

Definition 1.3 (Least Squares method[8]). *Let $y_1, y_2, \ldots, y_n$ be observed values and $\hat{y}_1(\theta), \hat{y}_2(\theta), \ldots, \hat{y}_n(\theta)$ be model predictions depending on parameters θ. The least squares method estimates θ by finding*

$$\min_{\theta} \sum_{i=1}^{n} \big(y_i - \hat{y}_i(\theta)\big)^2.$$

1.3 Structure of the paper

This paper will start from the exponential growth model in Section 2, which is the most fundamental description of population evolution under the assumption of unlimited resources. Then, in Section 3, the classic Logistic model will be introduced, and its practical application ability will be demonstrated by fitting the data of yeast population.

To overcome the limitations of the Logistic model, in Section 4 we further explore its extended forms, including the Richards model and the Gompertz model, to illustrate how modifications to the growth term alter the model's behavior, such as the inflection point position and curve shape, and to understand why these two models perform better than the logistic model in describing specific scenarios.

Furthermore, in Section 5, we will understand why one-dimensional models cannot generate oscillations and introduce the Lotka–Volterra model, which describes the interaction between species through a two-dimensional system and explains the periodic oscillation phenomenon in predator-prey systems. specifically, we also conduct fitting analysis with real data of hares and lynxes to demonstrate the feasibility of the Lotka–Volterra model.

Finally, in Section 6, several improvement directions will be proposed based on real biological phenomena, including the Allee effect and time-varying environmental carrying capacity, in an attempt to address the behaviors that the classical model fails to explain.

2 A simple approach: Exponential growth model

First consider an intuition: the increase in population size is related to the current population size; the larger the current population size, the more offspring can be produced. This leads to the simplest model: exponential growth.

The exponential growth model is

$$\frac{dx}{dt} = rx,$$

where r is a constant.

This is the simplest growth model. It assumes that the population grows at a rate proportional to its current size. Equivalently, the per-capita growth rate is constant:

$$\frac{x'}{x} = r.$$

Biologically, this means that resources are effectively unlimited, there is no crowding effect, and the environment does not change over time.

Solution and fixed point

We can easily find the explicit solution to this model: the explicit solution is

$$x(t) = x_0 e^{rt},$$

where $x_0 = x(0)$ is the initial population size. The only equilibrium is

$$x^* = 0.$$

The behavior depends on the sign of r:

- If $r > 0$, then for any initial value $x_0 > 0$, the solution grows monotonically and without bound.
- If $r < 0$, then the solution decays exponentially to 0.
- If $r = 0$, then every solution is constant.

Thus, when $r > 0$, the equilibrium $x = 0$ is unstable; when $r < 0$, it is asymptotically stable.

Limitations

Although this most fundamental model explains the relationship between population evolution and current quantity, its shortcomings are equally obvious. For instance, it allows the population to increase indefinitely over the long term, which is clearly unrealistic. Therefore, we introduce the most classic population evolution model: the Logistic model.

3 Classical Logistic Model

The classical logistic model is

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right),$$

where $r > 0$ is the intrinsic growth rate and $K > 0$ is the carrying capacity.[3]

The logistic model extends exponential growth by introducing a density-dependent correction term. The per-capita growth rate is

$$\frac{x'}{x} = r\left(1 - \frac{x}{K}\right)$$

As x increases, this rate decreases linearly. From a biological perspective, this means that as the population size expands, congestion and competition will become more intense. The parameter K represents the environmental carrying capacity, that is, the population size level that can be maintained in the long term.

Fixed points

Set the equation to zero to find the fixed points:

$$rx\left(1 - \frac{x}{K}\right) = 0,$$

so the fixed points are

$$x^* = 0 \qquad \text{and} \qquad x^* = K.$$

By linear stability analysis, for $r > 0$:

- $x = 0$ is unstable;
- $x = K$ is stable.

Thus, every positive solution approaches K as $t \to \infty$.

Explicit solution

The logistic equation also admits a solution that can be solved directly:

$$x(t) = \frac{K}{1 + Ae^{-rt}},$$

where A equals $\frac{K-x_0}{x_0}$ and is determined by the initial condition. This formula makes the sigmoidal shape of the logistic curve explicit.

Additional properties

The logistic curve has an inflection point at

$$x = \frac{K}{2}.$$

Proof. Consider the logistic differential equation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right).$$

Differentiating both sides with respect to t, we obtain

$$\frac{d^2x}{dt^2} = r\frac{dx}{dt}\left(1 - \frac{x}{K}\right) - \frac{r}{K}x\frac{dx}{dt}.$$

Factoring out $\frac{dx}{dt}$, this simplifies to

$$\frac{d^2x}{dt^2} = r\frac{dx}{dt}\left(1 - \frac{2x}{K}\right).$$

For a non-equilibrium solution, we have $\frac{dx}{dt} \neq 0$, so the inflection point occurs when

$$1 - \frac{2x}{K} = 0.$$

Solving for x, and

$$x = \frac{K}{2}.$$

□

This means that the population initially accelerates, then later decelerates as it approaches the carrying capacity. The model therefore produces a standard S-shaped growth curve.

Example: yeast population

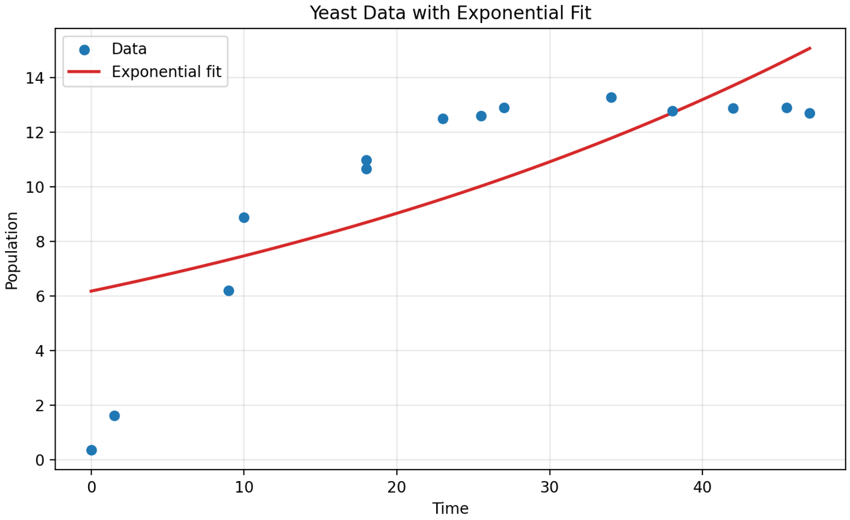
For the evolution of a single species under limited resources, the logistic model performs better than the exponential model. We use the following set of yeast data evolving over time for comparison.

t	$P(t)$	t	$P(t)$
0	0.37	25.5	12.60
1.5	1.63	27	12.90
9	6.20	34	13.27
10	8.87	38	12.77
18	10.66	42	12.87
18	10.97	45.5	12.90
23	12.50	47	12.70

Table 1: Yeast growth data[5]

Although the difference between the two can be intuitively felt from the visualization results, for mathematical rigor, we use RMSE to measure the accuracy of the two: Root Mean Square Error (RMSE) measures the average magnitude of prediction errors. The smaller the RMSE value, the better the model fits the data.

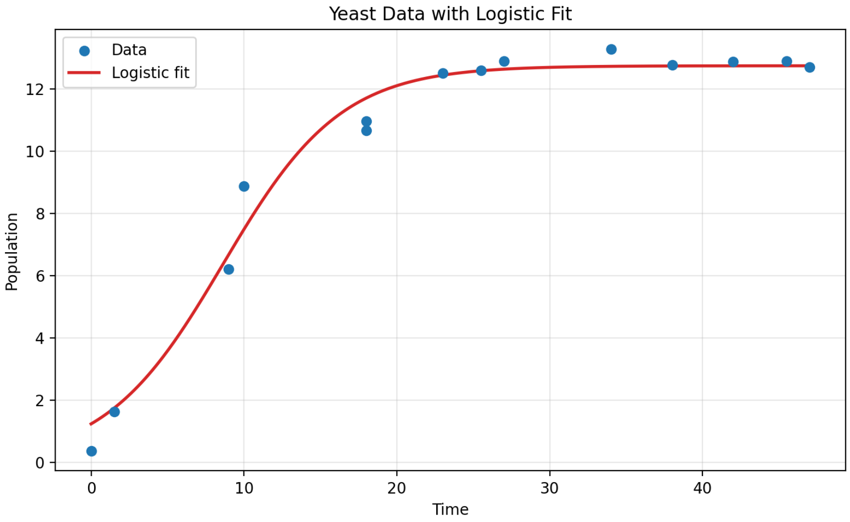
We fitted the yeast growth data using the nonlinear least squares method with the exponential model and the logistic model. Specifically, the parameters of each model were estimated by the `curve_fit` function in `SciPy`, which minimizes the sum of the squared residuals between the observed data and the model's predicted values. The fitting results are as follows:



x_0	r
6.1771	0.0190

$$RMSE_1 = 2.6988$$

Figure 1: Exponential model fit



K	x_0	r
12.7421	1.2344	0.2586

$$RMSE_2 = 0.5944$$

Figure 2: Logistic model fit

As there is $RMSE_1$=2.6988>$RMSE_2$=0.5944, we can confirm that logistic model fits the data better than exponential model, which is our desired result.

4 Several variations of Logistic model

Although Logistic model provided a good theoretical ”guess” of population, it has been criticized for many drawbacks. Notably, its inflection point is fixed at K/2; in other words, its shape is fixed, which means it has limited ability for shape changes due to complex external environmental effects.

In addition, the logistic model assumes that as long as the initial population is positive, it will gradually approach the carrying capacity over time. However, this is not true under high environmental pressure. Consider the growth of tumor cells in the human body: cancer cells face environmental pressure from the moment they are born, such as being hunted by immune cells, rather than when approaching the carrying capacity.

Therefore, we introduce two variants of the logistic model: the **Richards model** and the **Gompertz model**. They have improved the original logistic structure to try to solve the two problems mentioned above.

4.1 Richards model

A common generalization of the logistic model is the Richards model:

$$\frac{dx}{dt} = rx\left[1 - \left(\frac{x}{K}\right)^{\nu}\right],$$

where $\nu > 0$ is an additional shape parameter.[10]

The Richards model modifies the crowding term in the logistic equation. When $\nu = 1$, it reduces exactly to the classical logistic model. The extra parameter ν changes how quickly density dependence becomes important and allows more flexible sigmoidal shapes.

Fixed points

To find fixed points, let

$$rx\left[1-\left(\frac{x}{K}\right)^{\nu}\right]=0,$$

then fixed points are

$$x^*=0 \qquad \text{and} \qquad x^*=K.$$

For $r > 0$ and $\nu > 0$:

- if $0 < x < K$, then $x' > 0$;
- if $x > K$, then $x' < 0$.

Thus, positive solutions still move toward K, which is the same behavior of Logistic model.

Shape parameter

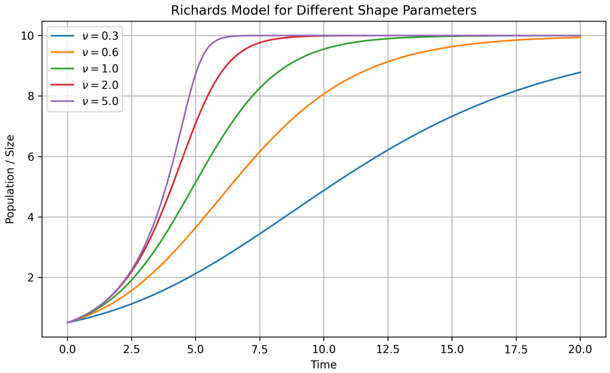


Figure 3: Richard model with different ν values

From the structure of the Richards model, it can be seen that its fixed points are consistent with those of the Logistic model. The difference lies in thatν can effectively change the shape of the Logistic model.

Inflection point

For the Richards model

$$\frac{dx}{dt}=rx\left[1-\left(\frac{x}{K}\right)^{\nu}\right],$$

the inflection point occurs at

$$x^*=K\left(\frac{1}{1+\nu}\right)^{1/\nu}.$$

Proof. Let

$$f(x) = rx\left[1 - \left(\frac{x}{K}\right)^{\nu}\right].$$

Then

$$\frac{d^2x}{dt^2} = f'(x)\frac{dx}{dt}.$$

Away from equilibrium points, the inflection point is determined by

$$f'(x) = 0.$$

Compute

$$f'(x) = r\left[1 - \left(\frac{x}{K}\right)^{\nu}\right] - rx \cdot \nu\left(\frac{x}{K}\right)^{\nu-1}\frac{1}{K}.$$

Simplifying,

$$f'(x) = r\left[1 - (1+\nu)\left(\frac{x}{K}\right)^{\nu}\right].$$

Setting $f'(x) = 0$ gives

$$\left(\frac{x}{K}\right)^{\nu} = \frac{1}{1+\nu},$$

hence

$$x = K\left(\frac{1}{1+\nu}\right)^{1/\nu}.$$

□

This aligns with the intuition: $\frac{d^2x}{dt^2}$ can be seen as describing the shape of the curve; change in the shape should also affect the inflection point.

4.2 Gompertz Growth Model

The Gompertz model[9] is commonly written as

$$\frac{dx}{dt} = rx\ln\left(\frac{K}{x}\right), \qquad x > 0.$$

In this model, the per-capita growth rate is

$$\frac{x'}{x} = r\ln\left(\frac{K}{x}\right).$$

Unlike the logistic model, where the per-capita growth rate decreases linearly with x, here it decreases logarithmically. This creates a different type of sigmoidal growth, visually more asymmetric than the logistic curve.

Fixed point

For positive populations, the fixed point is

$$x^* = K.$$

Indeed, if $x < K$, then $\ln(K/x) > 0$ and the population grows; if $x > K$, then $\ln(K/x) < 0$ and the population declines. Thus, positive solutions tend toward K.

Inflection point

For the Gompertz model

$$\frac{dx}{dt} = rx \ln\left(\frac{K}{x}\right),$$

we compute the second derivative to determine the inflection point.

Let

$$f(x) = rx \ln\left(\frac{K}{x}\right).$$

Then

$$\frac{d^2x}{dt^2} = f'(x)\frac{dx}{dt}.$$

Away from equilibrium, the inflection point is determined by

$$f'(x) = 0.$$

Compute the derivative:

$$f'(x) = r \ln\left(\frac{K}{x}\right) - r.$$

Setting $f'(x) = 0$ gives

$$\ln\left(\frac{K}{x}\right) = 1.$$

Solving for x, we obtain

$$x = \frac{K}{e}.$$

Thus, the inflection point occurs at

$$x^* = \frac{K}{e}.$$

This shows that, compared with the Logistic model, the Gompertz model reaches its maximum growth rate earlier. This shows as a more asymmetric, left-skewed shape curve:

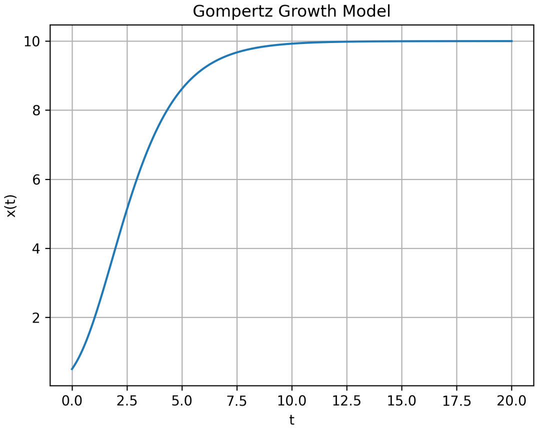


Figure 4: Gompertz model shape

This kind of curve is realistic when the survival pressure is high. For instance, we can imagine a herd of cattle on a land where resources are extremely scarce. Even before reaching the maximum number that the land can support, the pressure of food competition will already limit the growth rate of the animal population. Moreover, as mentioned earlier, tumor cells are also a good example: the human body's immune system will cause cancer cells to reach the maximum growth rate very quickly, and then they can no longer accelerate their growth.

5 Multi-groups model: Lotka–Volterra model

Motivation for higher-dimensional models

The one-dimensional autonomous differential equation

$$\frac{dx}{dt} = f(x)$$

is sufficient to describe simple growth processes such as exponential or logistic growth. However, such models are inherently limited: they cannot capture oscillatory behavior or interactions between multiple species.

In many biological systems, especially in the dynamic relationship between predators and prey, the population size often oscillates rather than showing a monotone behavior. This phenomenon stems from the interaction between species, where the growth of one population depends on the existence of another. For such effects, higher-dimensional systems are necessary.

Lemma 5.1 (No oscillation in one-dimensional autonomous systems). *Consider the autonomous differential equation*

$$\frac{dx}{dt} = f(x),$$

where f is locally Lipschitz continuous. Then any non-constant solution $x(t)$ is monotonic on its interval of existence. In particular, the system cannot exhibit sustained oscillations.

Proof. Let $x(t)$ be a non-constant solution. Then there exists some t_0 such that $f(x(t_0)) \neq 0$. By Lipcshitz continuity of f, there exists $\varepsilon > 0$ such that $f(x)$ has constant sign, $\forall x \in (x(t_0) - \varepsilon,\ x(t_0) + \varepsilon)$.

By continuity of $x(t)$, there exists $\delta > 0$ such that

$$x(t) \in (x(t_0) - \varepsilon,\ x(t_0) + \varepsilon), \quad \forall t \in (t_0 - \delta,\ t_0 + \delta).$$

Therefore, for all $t \in (t_0 - \delta,\ t_0 + \delta)$, we have either

$$\frac{dx}{dt} = f(x(t)) > 0 \quad \text{or} \quad \frac{dx}{dt} = f(x(t)) < 0,$$

which implies that $x(t)$ is strictly increasing or strictly decreasing in that interval.

Prove by contradiction. Suppose that $x(t)$ oscillates. Then it must attain both a local maximum and a local minimum at some times t_1 and t_2. At such points, we must have

$$\frac{dx}{dt}(t_1) = 0, \qquad \frac{dx}{dt}(t_2) = 0,$$

that is,

$$f(x(t_1)) = 0, \qquad f(x(t_2)) = 0.$$

Thus, both $x(t_1)$ and $x(t_2)$ are fixed points.

However, by uniqueness of solutions to autonomous differential equations, if a solution reaches a fixed point, it must remain there for all future time. This contradicts the assumption that $x(t)$ continues to vary.

Therefore, non-constant solutions cannot oscillate, and must be monotonic. $\square$

Now we introduce the classical Lotka–Volterra predator–prey model[1]:

$$\begin{cases} \dfrac{dx}{dt} = \alpha x - \beta xy, \\ \dfrac{dy}{dt} = -\gamma y + \delta xy, \end{cases}$$

where $x(t)$ denotes the prey population and $y(t)$ denotes the predator population. The parameters $\alpha, \beta, \gamma, \delta > 0$ represent interaction rates between the two species.

The Lotka–Volterra model describes the interaction between a prey species and a predator species. In the absence of predators, i.e., $y = 0$, the prey grows exponentially at rate α. In the absence of prey, i.e., $x = 0$, the predator population decays exponentially at rate γ.

The interaction terms βxy and δxy represent encounters between prey and predators. The term $-\beta xy$ reduces the prey population due to predation, while δxy increases the predator population through consumption of prey.

Fixed points

Set the system to zero:

$$\alpha x - \beta xy = 0, \qquad -\gamma y + \delta xy = 0.$$

Solving gives the fixed points:

$$(x^*, y^*) = (0, 0) \qquad \text{and} \qquad (x^*, y^*) = \left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right).$$

The stability of the fixed points can be analyzed using linearization.

- $(0, 0)$ is a saddle point and therefore unstable;
- $\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$ is a center, leading to closed orbits.

Thus, solutions near the nontrivial fixed point exhibit oscillatory behavior.

Conservative system

Lemma 5.2 (Lotka–Volterra model is conservative)**.** *The Lotka–Volterra system admits a conserved quantity of the form*

$$H(x, y) = \delta x - \gamma \ln x + \beta y - \alpha \ln y.$$

Proof. Write

$$\frac{dH}{dt} = \delta \frac{dx}{dt} - \gamma \frac{1}{x}\frac{dx}{dt} + \beta \frac{dy}{dt} - \alpha \frac{1}{y}\frac{dy}{dt}.$$

Substituting the system,

$$\frac{dx}{dt} = x(\alpha - \beta y), \qquad \frac{dy}{dt} = y(-\gamma + \delta x),$$

we obtain

$$\frac{dH}{dt} = (\delta x - \gamma)(\alpha - \beta y) + (\beta y - \alpha)(-\gamma + \delta x).$$

Expanding and simplifying yields

$$\frac{dH}{dt} = 0.$$

Thus $H(x, y)$ is conserved along trajectories. □

Example: Lynx and Hare

To compare the performance of different population models, we fit both the logistic model and the Lotka–Volterra model to the observed hare–lynx data using nonlinear least squares.

Year	Hare	Lynx
1847	21000	49000
1848	12000	21000
1849	24000	9000
1850	50000	7000
1851	80000	5000
⋮	⋮	⋮

Table 2: Hare and lynx population data[6]

For the logistic model, we use the explicit solution

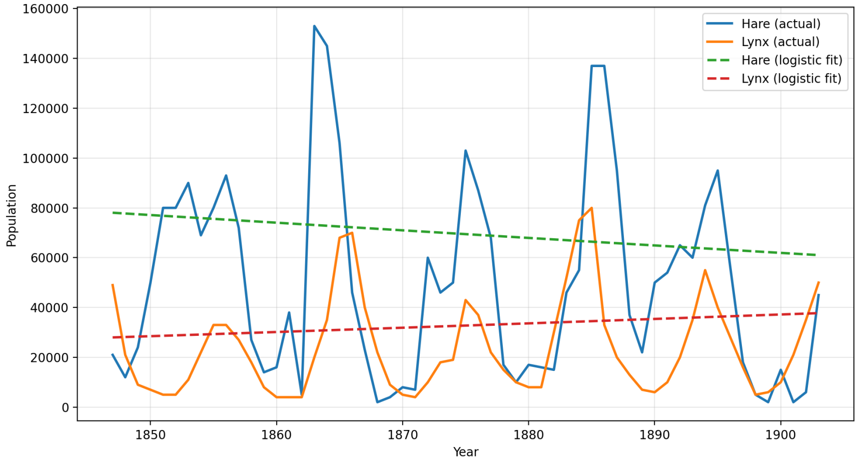
$$x(t) = \frac{K}{1 + Ae^{-rt}},$$

where the parameters K, r, and x_0 are estimated by minimizing the squared error between the model prediction and the observed data. The system is solved numerically using the `solve_ivp` routine from `scipy.integrate`. The residual is constructed from both prey and predator populations, with separate normalization to account for scale differences.

To avoid local minima, multiple initial parameter guesses are tried for both Logistic model and Lotka–Volterra model based on empirical characteristics of the data such as average population levels and oscillation periods, and the best solution is selected based on RMSE.

This fitting procedure allows for a fair comparison between models, highlighting the ability of the Lotka–Volterra system to capture oscillatory dynamics that cannot be reproduced by one-dimensional models.

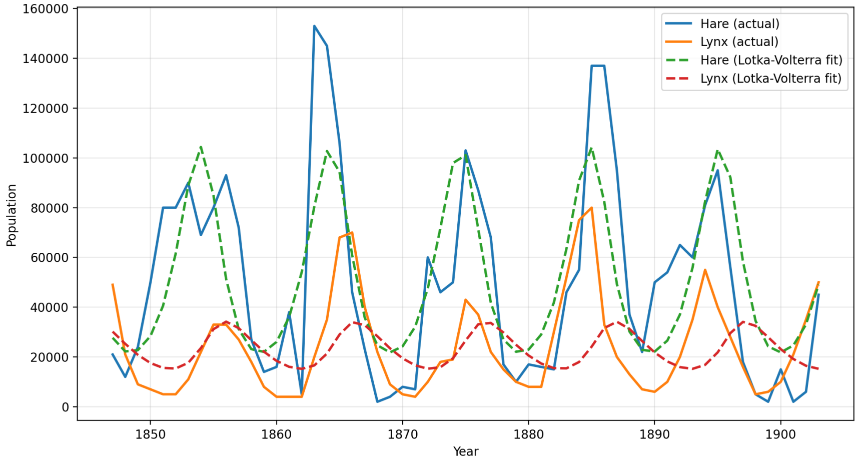
The result is as follow:



	K	x_0	r
Hare	153153.0000	78047.8440	-0.0080
Lynx	80080.0000	27996.3761	0.0090

$$RMSE_{\text{hare}} = 44051.2532, \quad RMSE_{\text{lynx}} = 21129.7877$$

Figure 5: Logistic model fit for hare and lynx populations



α	β	δ	γ
1.2000	0.00005120	0.00000625	0.3296

x_0 (hare)	y_0 (lynx)
27695.6259	30182.1519

$$RMSE_{\text{hare}} = 26529.3557, \quad RMSE_{\text{lynx}} = 19255.0414$$

Figure 6: Lotka–Volterra model fit for hare and lynx populations

Since the RMSE of the Logistic fit is larger than that of the Lotka-Volterra fit, the fitting effect of Lotka-Volterra is better. Additionally, from the visualization results, we can also intuitively find that Lotka-Volterra generates a distinct oscillation structure, which is impossible for the one-dimension flow Logistic model.

6 Several potential improvements

The classic one-dimensional population models discussed above, including the Logistic model, the Gompertz model and the Richards model, provide useful approximate descriptions of population dynamics. However, the generalization ability of these models is still limited; specifically, they do not reflect some real biological phenomena.

In this section, we propose some mathematically well-defined improvement measures that, while maintaining the analytical operability, enhance the adaptability of these models to certain real-world environmental factors, making their behavior more realistic.

6.1 Allee Effect

One important limitation of the classical Logistic model

$$x' = rx\left(1 - \frac{x}{K}\right)$$

is that it predicts positive growth for all population sizes $x > 0$.

The Allee effect is a concept in biology. It indicates that a biological population tends to disappear when it is below a certain threshold. This can be explained as the greater survival pressure faced by social animals when they are unable to collaborate, the difficulty in finding a mate, etc.[7]

To incorporate this mechanism, we could try to modify the logistic model by introducing a low-density threshold $A > 0$:

$$x' = rx\left(1 - \frac{x}{K}\right)\left(\frac{x}{A} - 1\right), \qquad 0 < A < K.$$

Notice that:

- When $0 < x < A$, we have $x' < 0$, so the population declines.
- When $A < x < K$, we have $x' > 0$, so the population grows.
- When $x > K$, we have $x' < 0$.

By solving $x' = 0$, fixed points are

$$x^* = 0, \quad x^* = A, \quad x^* = K.$$

and linear analysis shows that:

- $x = 0$ is locally stable,
- $x = A$ is unstable,
- $x = K$ is locally stable.

Thus, the system exhibits a threshold: if the initial population satisfies $x_0 < A$, the population tends to extinction, whereas if $x_0 > A$, it converges to the carrying capacity K. This bistable structure provides a more realistic description for populations subject to low-density risks based on basic Logistic model.

6.2 Dynamic carrying capacity

Another key limitation of the classical models is the assumption that the carrying capacity K is constant. In practice, environmental conditions such as seasons which often refers to resource availability, climate, and human intervention often vary over time, leading to a time-dependent carrying capacity.

To account for this, we consider the modified model

$$x' = rx\left(1 - \frac{x}{K(t)}\right),$$

where $K(t) > 0$ is a prescribed, locally Lipschitz continuous function of time. A typical example is a periodic environment:

$$K(t) = K_0\big(1 + \varepsilon \sin(\omega t)\big), \qquad 0 < \varepsilon < 1.$$

This formulation allows the model to capture seasonal or cyclic variations in environmental capacity. Compared with the autonomous Logistic model we learn from the class, the system becomes non-autonomous, and the long-term behavior is no longer characterized solely by fixed fixed points.

We can notice that this modified strucuture still have some great properties:

Lemma 6.1 (Existence and uniqueness)**.** *The R.H.S of the equation is continuous and locally Lipschitz in x. Therefore, for any initial value $x(0) = x_0$, the system admits a unique local solution.*

Proof. Define

$$f(t,x) = rx\left(1 - \frac{x}{K(t)}\right).$$

Since $K(t) > 0$ is Lipschitz continuous, the function $f(t,x)$ is continuous in both variables. Moreover, for fixed t,$K(t)$ can be treated as a constant and thus $f(t,x)$ is a polynomial in x, hence continuously differentiable in x, which implies local Lipschitz continuity in x. Then by the definition of Lipschitz continuous and Picard–Lindelöf theorem[2], the existence and uniqueness of solutions are ensured. □

Lemma 6.2 (Positivity)**.** *If $x(0) \geq 0$ and $K(t) > 0$, then the solution satisfies $x(t) \geq 0$ for all $t \geq 0$.*

Proof. First notice that $x = 0$ is a solution of the differential equation. If $x(t)$ were to become negative, it would have to cross zero at some time t^*. By uniqueness of solutions, the solution passing through $(t^*, 0)$ must be identically zero, which contradicts the assumption that $x(t)$ changes sign. Hence $x(t)$ remains nonnegative. □

Lemma 6.3 (Boundedness)**.** *Assume that $K(t)$ is bounded above by some constant $K_{\max} > 0$. Then any solution with $0 \leq x(0) \leq K_{\max}$ remains bounded for all $t \geq 0$.*

Proof. Let $K(t) \leq K_{\max}$. If $x(t) > K_{\max}$, then

$$x' = rx\left(1 - \frac{x}{K(t)}\right) \leq rx\left(1 - \frac{x}{K_{\max}}\right) < 0.$$

This is sufficient for proving that the solution won't grow beyond $K_{\max}$,i.e., $x(t)$ is bounded. □

Compare with the basic constant-K case, the system could present more complex behaviors such as periodic responses or delayed adjustment to environmental changes. This makes the model more suitable for fitting empirical data with seasonal and climatical changes.

Contribution

The entire project was completed independently.

Acknowledgements

The author acknowledges the use of OpenAI Codex for assistance in generating code used for simulation in this project.

The author also used ChatGPT to assist with brainstorming initial ideas.

References

[1] Mira C. Anisiu. Lotka, volterra and their model. *Didactica Mathematica*, 32(1), 2014.

[2] Earl A. Coddington and Norman Levinson. *Theory of Ordinary Differential Equations*. McGraw-Hill, 1955.

[3] Antonio Di Crescenzo and Paola Paraggio. Logistic growth described by birth-death and diffusion processes. *Mathematics*, 7(6):489, 2019.

[4] Rob J. Hyndman and Anne B. Koehler. Another look at measures of forecast accuracy. *International Journal of Forecasting*, 22(4):679–688, 2006.

[5] J. M. Mahaffy. Yeast models. `https://jmahaffy.sdsu.edu/courses/s02/math337/lectures/YeastModels/yeast.html`. Accessed: 2026.

[6] Michael Osthege. Lynx-hare dataset from leigh 1968. `https://gist.github.com/michaelosthege/27315631c1aedbe55f5affbccabef1ca`. Accessed: 2026.

[7] Phil A. Stephens, William J. Sutherland, and Robert P. Freckleton. What is the allee effect? *Oikos*, 87(1):185–190, 1999.

[8] Endre Süli and David F. Mayers. *An Introduction to Numerical Analysis*. Cambridge University Press, 2003.

[9] Kathleen M. C. Tjørve and Even Tjørve. The use of gompertz models in growth analyses, and new gompertz-model approach: An addition to the unified-richards family. *PLoS ONE*, 12(6):e0178691, 2017.

[10] X. S. Wang, J. Wu, and Y. Yang. Richards model revisited: Validation by and application to infection dynamics. *Journal of Theoretical Biology*, 313:12–19, 2012.