

# The Research History of Population Models

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**Abstract:** This paper mainly introduces the research history of biological population models, especially predator-prey models. With the proposal of the most traditional and representative Lotka-Volterra model, the dynamic behavior of biological population models has become increasingly clear. The three-dimensional Lotka-Volterra model has also played a pivotal role throughout the entire research process. Clearly, scholars' thirst for knowledge drives them to be unsatisfied with studying the traditional Lotka-Volterra model. They apply previous research methods to new biological population models, and have also achieved a considerable number of research results. However, with the continuous development of computer technology, numerical simulation has become an important tool for studying biological population models, which means that the impact of adding stochastic terms such as Brownian motion, time delays, and Levy jumps to the model can be intuitively presented. This paper summarizes the different stages of research on biological population models and briefly introduces the important theoretical achievements of different representative models.

**Keywords:** Predator-Prey Model, Lotka-Volterra Model, Food Chain Model, Brownian Motion, Time delay, Levy Jump.

## 1. Introduction

Population models are an important component of biomathematics. Population models help us understand how biological populations change and develop in natural environments, such as how species grow, fluctuate, or go extinct over time. By establishing and analyzing population models, we can predict future trends of populations, which is of great significance for wildlife management and conservation, agricultural pest control, and more. At the same time, population models can be used to study the dynamics of ecological processes, such as the interactions between predators and prey, competition and symbiotic relationships among species, and how these relationships influence species evolution, which can help us develop and refine ecological theories. In summary, population models in biomathematics are of significant scientific value and practical significance for understanding the behavior of biological populations, predicting future changes, formulating effective management strategies, and advancing ecological theory.

A population refers to a collection of individuals of the same species that occupies a specific area of space during a given time. The most important aspect of studying populations is their numerical changes, which include growth, fluctuation, stability, and decline. Population growth occurs in two basic patterns: exponential growth and logistic growth. Logistic growth refers to the fact that, as a population is relatively small, its growth will become faster. However, as the number of individuals increases, due to limited space, competition within the population becomes more intense, and resources become scarce. This leads to an increase in mortality rates and a decrease in birth rates until the population reaches a certain stable level.

In biomathematics, we often use a dynamical perspective to analyze objective phenomena within populations and to study the relationships between species and their environment, as well as between different species. In ecosystems, the interactions among predators, competition among predators, and the interplay between predators and prey constitute the three main types of interactions. Among these, competition is the most widely discussed. When two or more species

compete for the same prey or resources, this interaction occurs, and the resulting competition naturally inhibits the growth of species.

Volterra[1] was the first to propose a relatively complete theory of population competition and demonstrated that a biological population system with multiple predators preying on a single resource is impossible to coexist. This conclusion does not conform to people's intuition and has been questioned. However, this result has been applied to differential equations and was named the "competitive exclusion principle"[2] in the 1960s. The "competitive exclusion principle" further points out that  $n$  species cannot coexist on fewer than  $n$  resources. This conclusion has significantly advanced the research on biological population models.

## 2. Lotka-Volterra Model

Biomathematics has always been a hot topic for research, and the predator-prey model is a key component of biological population models. For a long time, there has been no suitable mathematical model to relatively accurately describe the relationship between predator and prey.

### 2.1. The Standard Lotka-Volterra Model

In 1925, the American mathematician Alfred J. Lotka (1880-1949) and the Italian mathematician Vito Volterra (1860-1940) collaborated to propose a model that could clearly describe the relationship between predators and prey. This model was later named after these two researchers and is known as the Lotka-Volterra model in subsequent research, often also referred to as the predator-prey model. This model laid the foundation for the theoretical framework of population biology, and subsequent scholars' research into the dynamic behavior of biological populations began with this model.

$$\begin{cases} \frac{dU}{dt} = \alpha U - \gamma UV, \\ \frac{dV}{dt} = -\beta V + e\gamma UV. \end{cases}$$

Figure 1. Standard Lotka-Volterra Model

The Lotka-Volterra model has a distinct characteristic—it does not diverge, but it also does not converge. Its initial conditions directly determine its long-term dynamical behavior. The population size always fluctuates between a fixed peak and a fixed valley, which is quite different from the usual tendency of ecosystems to reach a certain equilibrium state.

## 2.2. 3D Lotka-Volterra Model

Building on the standard two-dimensional Lotka-Volterra model, researchers have begun to focus on three-dimensional Lotka-Volterra models. J. Llibre and D. Xiao[3] were the first to study the global dynamical behavior of traditional 3D Lotka-Volterra models and they provided relatively complete theoretical results. They not only obtained the necessary and sufficient conditions for the validity of the competitive exclusion principle but also described the global dynamical behavior of three species in the infinite time. The results further indicate that the three species in the system exist in two coexistence states: periodic oscillation and steady state, with the specific state depending on the abundance of the prey.

$$\begin{cases} dS(t) = S(t)(b_1 - a_{11}S(t) - a_{12}X_1(t) - a_{13}X_2(t))dt, \\ dX_1(t) = X_1(t)(b_2 + a_{21}S(t))dt, \\ dX_2(t) = X_2(t)(b_3 + a_{31}S(t))dt. \end{cases}$$

Figure 2. 3D Lotka-Volterra Model

## 3. Other Predator-Prey Models

As more and more scholars dedicate their efforts to studying biological population models, the aforementioned research results have already fairly well elucidated the dynamic properties of the traditional Lotka-Volterra model. Consequently, scholars have begun to shift their focus to more general predator-prey models. For instance, adding terms for intraspecific competition, interspecific competition, considering nonlinear growth rates, imposing restrictions on different coefficients, and so on. Among these, two-dimensional and three-dimensional biological population models have been studied more extensively, as higher-dimensional models not only significantly increase the computational load and the difficulty of proof for scholars but also lack representativeness. To compensate for the lack of representativeness, scholars have turned their attention directly to n-dimensional food chain models. Although these biological population models are quite idealized, they are highly representative and have yielded many promising research results.

### 3.1. 3D Predator-Prey Models

Since A.J. Lotka and V. Volterra proposed the predator-prey system, countless scholars have dedicated themselves to studying the Lotka-Volterra model and its modified forms. When considering the deterministic three-dimensional Lotka-Volterra model, scholars have achieved considerable theoretical results in terms of the existence conditions of its solutions and their behaviors. Koch [4] was the first to use numerical simulation to consider coexistence and concluded the possibility of two predators competing for renewable resources. McGehee and Armstrong [5] were the first to demonstrate the possibility of two predators coexisting on the same resource. However, none of these studies could clearly specify the parameter range for the coexistence of predators and prey.

J. Butler, et al[6] analyzed a mathematical model of two predators feeding on a single prey grown in a thermostat. They obtained results for global stability in the case where one of the predators goes extinct. Under appropriate conditions, it can be proven using bifurcation theorems that the predators can coexist in the form of limit cycles.

S.B. Hsu and S. P. Hubbell[7] studied the competition models between two predators and one prey. They systematically discussed the issue of coexistence of species under different conditions. They assumed that in the absence of predators, the prey population grows logistically, and predators have a saturated functional response to prey density when consuming them. When given the intrinsic growth rate of the prey and the predation intensity parameters of the predators, conditions for the survival or extinction of different species can be provided. They further pointed out that the key to the survival or extinction of different species mainly depends on the environmental carrying capacity of the prey. For a wide range of parameters, coexistence is also possible, but only as a periodic solution. They noted that coexistence will only appear when predators have a smaller birth-death ratio and simultaneously a smaller half-saturation constant.

$$\frac{dS(t)}{dt} = \gamma S(t)[1 - S(t)/K] - \left(\frac{m_1}{y_1}\right)\left(\frac{x_1(t)S(t)}{a_1 + S(t)}\right) - \left(\frac{m_2}{y_2}\right)\left(\frac{x_2(t)S(t)}{a_2 + S(t)}\right),$$

$$\frac{dx_1(t)}{dt} = \frac{m_1 x_1(t)S(t)}{a_1 + S(t)} - d_1 x_1(t),$$

$$\frac{dx_2(t)}{dt} = \frac{m_2 x_2(t)S(t)}{a_2 + S(t)} - d_2 x_2(t),$$

Figure 3. 3D Predator-Prey Model

### 3.2. N-Dimension Food Chain Models

Food chain Model is a special models of biological populations, consisting of n-1 predators and one prey. Each predator simultaneously feeds on a predator of one level lower. This means that each predator interacts with a maximum of two other species. Figure 4 shows a classic food chain model.

$$\begin{aligned} dx_1(t) &= x_1(t)(a_{10} - a_{11}x_1(t) - a_{12}x_2(t)) dt \\ dx_2(t) &= x_2(t)(-a_{20} + a_{21}x_1(t) - a_{23}x_3(t)) dt \\ &\vdots \\ dx_{n-1}(t) &= x_{n-1}(t)(-a_{n-1,0} + a_{n-1,n-2}x_{n-2}(t) - a_{n-1,n}x_n) dt \\ dx_n(t) &= x_n(t)(-a_{n0} + a_{n,n-1}x_{n-1}(t)) dt. \end{aligned}$$

Figure 4. N-Dimension Food Chain Model

A. Hening and D. H. Nguyen [8] considered the issue of the evolution of food chains in stochastic environments. Their assumption was that there is no intraspecific competition among predators. Under this assumption, they provided the conditions for persistence and extinction of this food chain. Subsequently, considering the case where there is competition within the predator population, the study showed that the extinction of species and the convergence of species can be determined by the invasion rate of predators.

## 4. Stochastic Predator-Prey Models

Ecosystems are often affected by environmental noise. In

recent years, to more accurately describe ecosystems, an increasing number of stochastic population models [9-11] have been proposed as supplements to some deterministic population models. In fact, stochastic population models are more practically meaningful and closer to real-world applications than deterministic population models, making research on stochastic population models meaningful and indispensable.

There are three common stochastic population models, namely, models with Brownian motion, time-delayed stochastic models, and Levy jump stochastic models. Of course, scholars have also proposed other stochastic population models. This section will introduce the main research results of the three common population models.

#### 4.1. Stochastic Models with Brownian Motions

When considering stochastic predator-prey models with Brownian motion, although many scholars have already considered perturbing the models by adding Brownian motion to different coefficients, there is still a lack of conclusive findings regarding the necessary and sufficient conditions for species coexistence and extinction. D.H. Nguyen and G. Yin [12] have derived sufficient conditions for coexistence and exclusion in a two-dimensional stochastic competitive Lotka-Volterra model, which approach necessary conditions. Furthermore, they have also proven the convergence of the distribution of positive solutions for the model.

$$\begin{cases} dX(t) = X(t)(a_1 - b_1X(t) - c_1Y(t))dt \\ \quad + (\alpha_1X^2(t) + \gamma_1X(t))dB_1(t) + \beta_1X(t)Y(t)dB_2(t), \\ dY(t) = Y(t)(a_2 - b_2Y(t) - c_2X(t))dt \\ \quad + (\alpha_2Y^2(t) + \gamma_2Y(t))dB_3(t) + \beta_2X(t)Y(t)dB_2(t), \end{cases}$$

**Figure 5.** 2D Predator-Prey Model with Brownian Motions

Li and S. Guo[13] considered a new method that differs from existing methods to analyze the stochastic persistence and extinction of predator-prey models with general functional responses, as well as the random factors that simultaneously affect the intrinsic growth rate and the rate of intraspecific interactions. Meanwhile, they also studied the existence of stationary distributions and the weak convergence to boundary processes in their paper. Through numerical simulations, they found that an appropriate intensity of white noise may allow predators and prey populations to fluctuate around their deterministic equilibrium values; however, too intense white noise may lead to the extinction of the predators and/or prey populations, which are the very reasons why it is meaningful to add stochastic perturbations to the model.

S.Zhang and X. Liu, et al. [14] have proven the existence of solutions for a 3D stochastic Lotka-Volterra model and provided sufficient conditions for coexistence. They then verified these conclusions through numerical simulations.

$$\begin{cases} dS(t) = S(t)(b_1 - a_{11}S(t) - a_{12}X_1(t) - a_{13}X_2(t))dt + \sigma_1S(t)dB_1(t), \\ dX_1(t) = X_1(t)(b_2 + a_{21}S(t) - a_{22}X_1(t) - a_{23}X_2(t))dt + \sigma_2X_1(t)dB_2(t), \\ dX_2(t) = X_2(t)(b_3 + a_{31}S(t) - a_{32}X_1(t) - a_{33}X_3(t))dt + \sigma_3X_2(t)dB_3(t). \end{cases}$$

**Figure 6.** 3D Predator-Prey Model with Brownian Motions

#### 4.2. Stochastic Models with Time Delays

Many scholars have dedicated their efforts to studying stochastic predator-prey models with time delay, for example,

J. Geng, M. Liu, and Y. Zhang[15] proposed a stochastic model with time delay for a single predator and two prey. They employed asymptotic methods to study the stability of the model in distribution and established clear criteria for the stability of the distribution.

$$\begin{cases} dX_1(t) = X_1(t)(b_1 - c_{11}X_1(t) - c_{12}X_2(t - \tau_{12}) - c_{13}X_3(t - \tau_{13}))dt, \\ dX_2(t) = X_2(t)(b_2 - c_{21}X_1(t - \tau_{21}) - c_{22}X_2 - c_{23}X_3(t - \tau_{23}))dt, \\ dX_3(t) = X_3(t)(-b_3 + c_{31}X_1(t - \tau_{31}) + c_{32}X_2(t - \tau_{32}) - c_{33}X_3(t))dt. \end{cases}$$

**Figure 7.** 3D Predator-Prey Model with Time Delays

R. Tan, H. Xiang, et al [16] studied a class of stochastic population competition systems with time delays. They first provided a proof of the existence of the unique positive solution for the system, then pointed out that the solutions of the system are stochastically bounded, and presented sufficient conditions for the global attractiveness of the system. At the same time, in their study, they found that with the increase of noise intensity, the species in the model will go extinct with probability 1.

#### 4.3. Stochastic Models with Levy Jumps

Clearly, the stochastic population models with Levy jumps are less studied than the two categories of models discussed in the previous section. Nevertheless, some scholars have achieved promising research results. For example, M. Liu and C. Bai[17] studied a one-predator-two-prey model with both white noise and Levy jumps. They first conducted a nearly complete parameter analysis of the model. In each case, the paper demonstrates that each species either persists or goes extinct at the mean, depending on some critical values. Based on this, they established sufficient criteria for the stability of the model's distribution.

$$\begin{cases} dN_1(t) = N_1(t^-)[r_1 - a_{11}N_1(t^-) - a_{12}N_2(t^-) - a_{13}N_3(t^-)]dt \\ \quad + \alpha_1N_1(t^-)dW(t) + \int_{\mathbb{Y}} N_1(t^-)\eta_1(u)\tilde{\Lambda}(dt, du), \\ dN_2(t) = N_2(t^-)[r_2 + a_{21}N_1(t^-) - a_{22}N_2(t^-) - a_{23}N_3(t^-)]dt \\ \quad + \alpha_2N_2(t^-)dW(t) + \int_{\mathbb{Y}} N_2(t^-)\eta_2(u)\tilde{\Lambda}(dt, du), \\ dN_3(t) = N_3(t^-)[r_3 + a_{31}N_1(t^-) - a_{32}N_2(t^-) - a_{33}N_3(t^-)]dt \\ \quad + \alpha_3N_3(t^-)dW(t) + \int_{\mathbb{Y}} N_3(t^-)\eta_3(u)\tilde{\Lambda}(dt, du), \end{cases}$$

**Figure 8.** 3D Predator-Prey Model with Levy Jumps

In particular, some scholars have simultaneously added Levy jumps and time delays to biological population models. For example, T. Ma, X. Meng, and Z. Chang [18] studied a one-predator-two-prey stochastic model that simultaneously possesses both types of stochastic terms. By utilizing the relevant theory of stochastic differential equations, he obtained sufficient conditions for the survival or extinction of the three species. Furthermore, through analyzing the asymptotic invariant distribution of the populations, the changes in the population's sustained levels were studied, followed by the derivation of conditions for global attractiveness and distributional stability. Using research methods based on partial differential equations, some promising theoretical results were obtained.

$$\begin{aligned}
dx_1(t) &= x_1(t) [a_1 - h_1 - a_{11}x_1(t) - a_{12}x_2(t - \tau_{12}) \\
&\quad - a_{13}x_3(t - \tau_{13})] dt + \sigma_1 x_1(t) dB_1(t) + x_1(t) \\
&\quad \cdot \int_{\mathbb{Y}} \gamma_1(v) \tilde{N}(dt, dv), \\
dx_2(t) &= x_2(t) [a_2 - h_2 - a_{21}x_1(t - \tau_{21}) - a_{22}x_2(t) \\
&\quad - a_{23}x_3(t - \tau_{23})] dt + \sigma_2 x_2(t) dB_2(t) + x_2(t) \\
&\quad \cdot \int_{\mathbb{Y}} \gamma_2(v) \tilde{N}(dt, dv), \\
dx_3(t) &= x_3(t) [-a_3 + a_{31}e^{-a_3\tau_{31}}x_1(t - \tau_{31}) \\
&\quad + a_{32}e^{-a_3\tau_{32}}x_2(t - \tau_{32}) - a_{33}x_3(t)] dt \\
&\quad + \sigma_3 x_3(t) dB_3(t) + x_3(t) \int_{\mathbb{Y}} \gamma_3(v) \tilde{N}(dt, dv).
\end{aligned}$$

**Figure 9.** 3D One-Predator-Two-Prey Model with Levy Jumps and Time Delays

## 5. Conclusion

This paper primarily summarizes the research journey of scholars on predator-prey models. Since the Lotka-Volterra model was proposed, scholars have conducted in-depth research on the model from various aspects, and the research results have had varying degrees of inspirational significance for all aspects and industries in real life. Starting with considering traditional Lotka-Volterra model with different coefficients, scholars moved on to consider higher-dimensional models. Furthermore, scholars have not been satisfied with this and have begun to consider n-dimensional biological population models, represented by n-dimensional food chain models.

With the continuous development of computer technology and the maturation of numerical simulation techniques, stochastic population models have taken center stage. After adding stochastic terms such as Brownian motion, time delays, and Levy jumps to deterministic biological population models, new models have been constructed. The stochastic population models with different stochastic terms have connections and differences, which provide scholars with a lot of room for innovation. To this day, stochastic models remain a hot topic of research, and scholars, using the initial methods of studying stochastic biological population models, have applied them to stochastic models in other fields and have also achieved satisfactory results.

## Acknowledgments

Throughout the writing of this entire thesis, I have gained a lot of valuable knowledge and experiences that go beyond the realm of learning, enriching my graduate school life.

I would like to thank my graduate advisor for guiding me. She provided continuous intellectual support and encouragement throughout the project, helping me overcome one obstacle after another.

At the same time, I also want to thank my fellow students for their assistance. When my thesis progress stagnated, it was their advice that helped me move forward.

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