A study on the Ecosystem of the Lampreys Based on Lotka-Volterra Modeling

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Abstract. This study provides insights into the ecosystem impacts of adaptive sex ratio variation in lampreys through mathematical and ecological modeling. The predator-prey relationship between prey, lampreys and indigenous populations was simulated using the Lotka-Volterra model, revealing the effect of increasing male sex ratio on the significant increase in prey population size and the variation in the three population cycles. The model was further linearized to determine the stability of the ecosystem under different sex ratios by calculating Jacobi matrices and eigenvalues and found that the ecosystem tends to be stable when the male ratio is within a specific range. Analysis of the model with the addition of parasites showed that an increase in male ratio promotes an increase in prey population size, has a smaller effect on competitors, and slightly reduces parasite numbers. These findings provide an important reference for understanding the effects of adaptive sex ratio variation on ecosystems and population interactions.

Keywords: Lotka-Volterra; linear stability theorem; dynamic systems.

1. Introduction

The aim of this paper is to explore the effects of adaptive sex ratio variation on ecosystems with the lampreys. Lampreys are influenced by food availability and thus sex determination during the larval stage, and this sex ratio variation may significantly affect their ecological roles and interactions with other species [1]. Through mathematical and ecological modeling, we investigated the ecological effects of sex ratio variation in lampreys. With the help of the Lotka-Volterra model, we simulated predator-prey relationships among prey, lampreys, and indigenous populations, revealing the effects of sex ratio variation on population abundance and periodicity. The effects of sex ratio variation on ecosystem stability were further analyzed, and it was found that ecosystems were more stable within a specific sex ratio range. By adding parasites to the modeling analysis, we found that an increase in male sex ratio affects prey population size, has a smaller effect on competitors, and slightly reduces parasite populations. These findings will contribute to a deeper understanding of the effects of adaptive sex ratio variation on ecosystems and population interactions.

2. Analysing Ecological Impacts Based on the Lotka-Volterra Model

First, we tried to use the Lotka-Volterra model to study the predation relationship between the food chain of prey, lampreys, and indigenous people [2].

We assume that the resources required for the survival of the prey are always abundant and that if there are no natural enemies, their populations can keep reproducing with an exponential growth rate and a natural growth rate α .

For lampreys, if there are no more preys, they will starve to death due to a lack of food resources, and the natural growth rate is negative, so γ_1 the equation can be visualized as the natural mortality rate of the lamprey's population.

For the indigenous people, the lamprey serves as an important food source. If the number of lampreys is scarce, the indigenous people will starve to death due to the lack of food resources. The rate of natural growth will be negative, so γ_2 in the equation can be imagined as the natural mortality rate of the indigenous people.

Lampreys and aborigines have different predation efficiencies when feeding on prey. β_1, β_2 Represent the predation efficiencies of lampreys and indigenous people, respectively.

Considering that there is an energy conversion efficiency when a predator feeds, i.e., the portion of the captured energy that is used for population reproduction, δ_1, δ_2 represents the increase in the survival rate of lampreys and of aborigines, respectively, because of predation.

Lotka-Volterra equation:

The population size $x(t)$ for preys, $y(t)$ for lampreys, and $z(t)$ for indigenous people over time t is given by the following Lotka-Volterra equation:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x(t) - \beta_1 x(t) y(t) \\ \frac{dy}{dt} &= \delta_1 x(t) y(t) - \gamma_1 y(t) - \beta_2 y(t) z(t) \\ \frac{dz}{dt} &= \delta_2 y(t) z(t) - \gamma_2 z(t)\end{aligned} \tag{1}$$

Where α : the natural growth rate of prey, β_1 : the probability that the prey are preyed upon, β_2 : the efficiency of indigenous people predation on lampreys, γ_1 : the natural mortality of lampreys, excluding human predation, γ_2 : the natural mortality rate of the indigenous population, δ_1 : the increased survival rate of lampreys due to prey eating, δ_2 : the increased survival of indigenous populations as a result of eating lampreys

According to the literature, the sex ratio of lampreys can vary depending on the external environment [3]. In environments where food is less available, the proportion of males can reach about 78 percent of the population. In environments where food is more readily available, the proportion of males is observed to be about 56 percent of the population.

Checking the related information, we found that different sexes of lampreys showed variability in the amount of food required [4], so we defined the efficiency of the lampreys' predation on prey as:

$$\beta_1 = k \cdot i + c \tag{2}$$

i Is the sex ratio of male lampreys to the population of lampreys?

For this system of nonlinear differential equations, we use an ode45 solver in MATLAB to solve it, and the result is shown in Fig. 1.

We set that $k = -0.5, c = 0.5,$ s.t. $\beta_1 = -0.5i + 0.5$

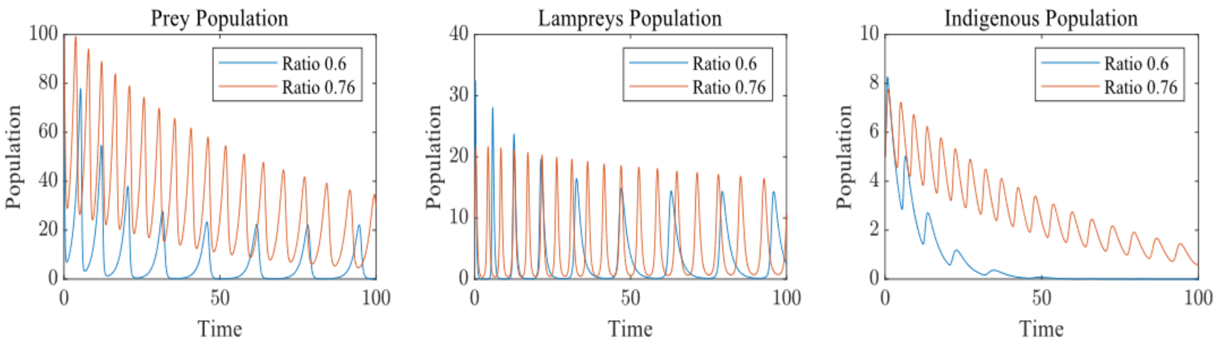


Fig 1. Curves of the abundance of praise, lampreys, and indigenous people as a function of time at male ratios of 0.6 and 0.76 for lampreys.

Typically, female lampreys need to consume more food to supply the energy needed to reproduce, and when the proportion of females increases, the proportion of males decreases, and the efficiency of predation on prey increases in the population of lampreys, which is consistent with our knowledge.

By analyzing Fig. 1, we can easily see that when the sex ratio is changed, the number of prey, lampreys, and indigenous inhabitants are all changed to different degrees.

There was a significant increase in the overall population of prey when the male sex ratio increased, and there was a more significant increase in both the maximum and minimum values, with an overall decreasing trend. There was also a significant level of increase in the indigenous people population, which also showed an overall decreasing trend. The lamprey population showed a slight increase in numbers and showed a more stable periodicity. All three patterns showed a decreasing trend in cycles.

In conclusion, changes in the sex ratio of lamprey's populations have a significant effect on the ecosystem.

3. Eigenvalue Method for Determining Ecosystem Stability

Next, the paper explores the impact on the stability of the ecosystem, given the changes in the sex ratios of lampreys.

In a previous paper, we used the Lotka-Volterra model to simulate the dynamic interactions between prey and lampreys. Changes in the sex ratio of lampreys were found to affect the ecosystem, and eventually, the number of races reached an equilibrium. Naturally, a question needs to be considered when analyzing the stability of its equilibrium point: Will the dynamic process between preys and lampreys return to its equilibrium point under sex ratio-induced perturbations?

We used the linear stability method to go about the determination, which is often used in the analysis of dynamic systems [5]. We use it to determine the stability of an ecosystem. The stability of an ecosystem at a given lampreys sex ratio is assessed in two ways: whether the state is equilibrium or not and the response speed of return to equilibrium after a perturbation. However, the Lotka-Volterra model, being a nonlinear dynamical equation, mostly does not have analytical solutions. Therefore, the nonlinear equation is linearized by us. By calculating the Jacobian matrix for the nonlinear equation, we can obtain the eigenvalues. The stability of the nonlinear system is determined from the real number of the eigenvalues in the linear system by the linear stability theorem. If the real number of all eigenvalues is less than zero, the system is stable. If there are eigenvalues whose real number is greater than zero, the system is unstable.

The linear stability theorem is used to analyze the stability of the population sizes of prey and lampreys in the previously established Lotka-Volterra model. The perturbation to the stability of the ecosystem is the changes in the sex ratio of lampreys.

$$\begin{aligned} &\beta_1 = k \cdot i + c \frac{dx}{dt} = \alpha \cdot x(t) - \beta_1 \cdot x(t) \cdot y(t) \\ &\frac{dy}{dt} = \delta_1 \cdot x(t) \cdot y(t) - \gamma_1 \cdot y(t) - \beta_2 \cdot y(t) \cdot z(t) \\ &\frac{dz}{dt} = \delta_2 \cdot y(t) \cdot z(t) - \gamma_2 \cdot z(t) \end{aligned} \tag{3}$$

Adding perturbations due to changes in the sex ratio of lampreys to the Lotka-Volterra model used in the first part,

$$w(t) = s(t) + q(t), \quad s = x, y, z \tag{4}$$

Where $s(t)$ denotes the state of praise, lampreys, and humans at moment t, $q(t)$ denotes the perturbation induced by the change in the sex ratio of lampreys at moment t, and $w(t)$ denotes the state of each species triggered by the perturbation.

After $w(t)$ is linearized. The general form $q(t)$ can be obtained as follows,

$$q_i = q_{i0} \cdot e^{\lambda t}, \quad i = 1, 2, ..., S \tag{5}$$

Where λ is the eigenvalue of the Jacobian matrix of a system of nonlinear equations?

If the real number of all eigenvalues λ are less than 0, as time passes:

$$\lim_{t \to \infty} \|q_i\| = 0 \tag{6}$$

The perturbation q_i will approach 0. The system returns to equilibrium. If there is an eigenvalue λ with a real number greater than 0, as time passes:

$$\lim_{t\to\infty}\|q_i\| = \infty \tag{7}$$

The perturbation q_i will increase infinitely. The system cannot return to equilibrium.

In addition to those, the response speed of the system can be judged based on the magnitude of the absolute value of the real part of the eigenvalues.

The Jacobian matrix for this system of nonlinear equations is (each row element in the matrix represents a first-order derivative concerning the number of each species in each differential equation):

$$B = \begin{pmatrix} \alpha - \beta_1 \cdot y(t) & -\beta_1 \cdot x(t) & 0 \\ \delta_1 \cdot y(t) & \delta_1 \cdot x(t) - \gamma_1 - \beta_2 \cdot z(t) & -\beta_2 \cdot y(t) \\ 0 & \delta_2 \cdot z(t) & \delta_2 \cdot y(t) - \gamma_2 \end{pmatrix} \tag{8}$$

In summary, it is only necessary to determine the positivity and negativity of the eigenvalues in the Jacobian matrix. Then, we can see whether the ecosystem is stable in that lamprey's sex ratio state.

Table 1. The eigenvalues of i Jacobian matrix.

Lamprey's male ratio	λ_1	λ_2	λ_3
0.56	-0.547	-0.206	-0.058
0.58	-0.201+0.031i	-0.191+0.023i	-0.12442
0.6	-0.024	-0.194	-0.169
0.62	0.179	-0.195+0.008i	-0.232+0.013i
0.64	0.287	-0.204+0.005i	-0.231+0.012i
0.66	0.364	-0.197	-0.219
0.68	0.423	-0.190	-0.228
0.70	0.468	-0.175	-0.234
0.72	0.502	-0.135	-0.237
0.74	0.517	-0.017	-0.239
0.76	0.407+0.130i	0.324+0.153i	-0.236
0.78	0.719+0.464i	0.641+0.378i	-0.196

Through the Table.2, when the sex ratio of lampreys is in the range of 0.56-0.60, the eigenvalues of its Jacobian matrix are all less than 0, which indicates that the ecosystem is still in a stable state in the case of perturbation triggered by the change of sex ratio. However, when the sex ratio is greater than 0.60, the ecosystem is not in a stable state. Meanwhile, by comparing the magnitude of the eigenvalues, when the sex ratio is equal to 0.56, the number of preys have the most rapid response rate to the disturbance. When the sex ratio is equal to 0.78, the number of lampreys has the most rapid response rate to the disturbance. These analyses are also consistent with common sense. When the sex ratio of lampreys is close to 0.5, this means that there is enough food for lampreys. However, a high proportion of males means that there is more food for lampreys, which leads to a stronger tendency for lampreys to reproduce and an increase in the proportion of females.

4. Improved Model to Simulate the Number of Parasites

According to the literature review, the interspecific relationship between parasites and lampreys may be competition, predation, or parasitism [6]. Therefore, we assume that there are three types of parasites in the same environment as lampreys.

Parasite 1: predation. Parasite 2: competition. Parasite 3: parasitism.

Moreover, in predatory relationships, female lampreys play a greater role, while in competitive relationships, male lampreys play a greater role. In parasitic relationships, both female and male lampreys may be parasitized.

Based on the first three questions, we added parameter k, which means the ability of lampreys to eliminate three types of parasites. Considering the different interspecific relationships between the three parasites and lampreys, we set the initial value $k_1 = 0.05,\ k_2 = 0.04, k_3 = 0.03$.

The growth rates of the three types of parasites are:

$$\begin{aligned} \frac{dP_1}{dt} &= r_{p1} \cdot P_1 \cdot (1 - \frac{P_1}{K_{p1}}) - S_{p1} \cdot P_1 - N_f \cdot k_1 \cdot P_1 \\ \frac{dP_2}{dt} &= r_{p2} \cdot P_2 \cdot (1 - \frac{P_2}{K_{p2}}) - S_{p2} \cdot P_2 - N_m \cdot k_2 \cdot P_2 \\ \frac{dP_3}{dt} &= r_{p3} \cdot P_3 \cdot (1 - \frac{P_3}{K_{p3}}) - S_{p3} \cdot P_3 - (N_f + N_m) \cdot k_3 \cdot P_3 \end{aligned} \tag{9}$$

Considering that lampreys may become infected and die after being parasitized or preying on parasites, we introduce the mortality rate ω of parasites on lampreys to calculate the population changes of lampreys further accurately. Moreover, we set the $\omega = 0.05$.

The growth rates of female and male lampreys are,

$$\begin{aligned} \frac{dN_f}{dt} &= r_f \cdot N_f (1 - \frac{N_f}{K_f}) - S_f \cdot N_f - \omega \cdot N_f \cdot (k_1 \cdot P_1 + k_3 \cdot P_3) \\ \frac{dN_m}{dt} &= r_m \cdot N_m (1 - \frac{N_m}{K_m}) - S_m \cdot N_{m1} - \omega \cdot N_m \cdot (k_2 \cdot P_2 + k_3 \cdot P_3) \end{aligned} \tag{10}$$

Where N_f and N_m: the number of female and male lampreys, respectively. r_f and r_m: The birth rates of female and male lampreys, respectively. K_f and K_m: The population capacity of female and male lampreys, respectively. S_f and S_m: The death rates of female and male lampreys, respectively. P_1, P_2 and P_3: The quantities of three types of parasites, respectively. r_{p1}, r_{p2} and r_{p3}: The birth rates of three types of parasites, respectively. K_{p1}, K_{p2} and K_{p3}: The population capacity of three types of parasites, respectively. S_{p1}, S_{p2} and S_{p3}: The death rates of three types of parasites, respectively. k_1, k_2 and k_3: The predation rates of three types of parasites, respectively. ω: The death rate of lampreys after consuming parasites or being parasitized.

We assume that the available resources are gradually decreasing, the male proportion of the lamprey population will gradually increase over time.

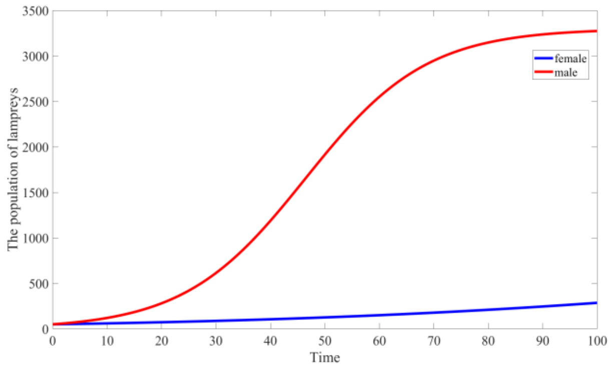


Fig 2. Changes in population size of lampreys when gender ratio changes.

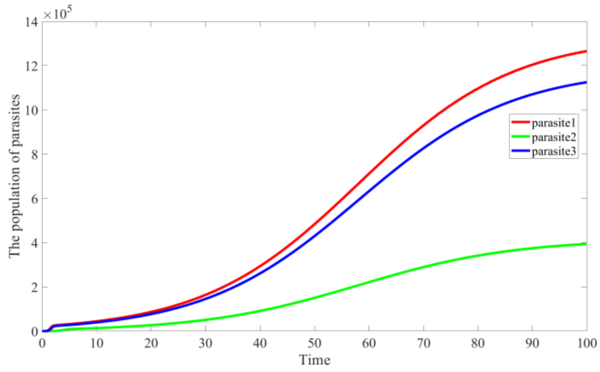


Fig 3. Changes in the population of parasites when the gender ratio changes.

From Fig. 2 and Fig. 3, parasite 1 has a predatory relationship with lampreys, and female lampreys have a greater impact on predatory parasites. Therefore, when the proportion of females decreases, the growth rate of the first type of parasite is the fastest. Parasite 2 is a competitive relationship, and male lampreys play the most important role in competition. Therefore, when the proportion of males increases, the growth rate of this parasite is the slowest. Parasite 3 is parasitic, which can parasitize both male and female fish, with a moderate growth rate.

We also considered the impact on three types of parasites when the gender ratio of the lamprey population remains unchanged and compared it with the change in gender ratio. Due to a relatively balanced gender ratio, which is conducive to reproduction, the overall population of lampreys will increase, and changes in the total number will also have a certain impact on parasites.

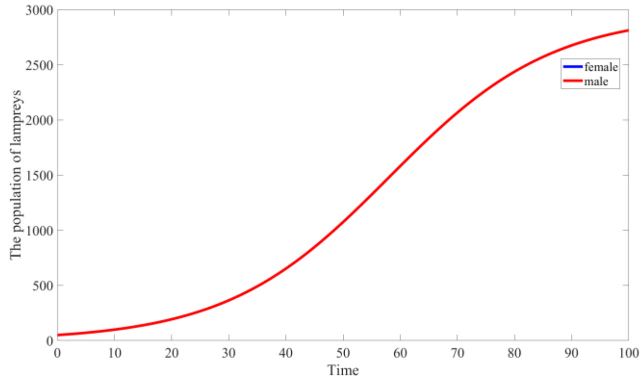


Fig 4. Changes in the population size of lampreys when the gender ratio is stable.

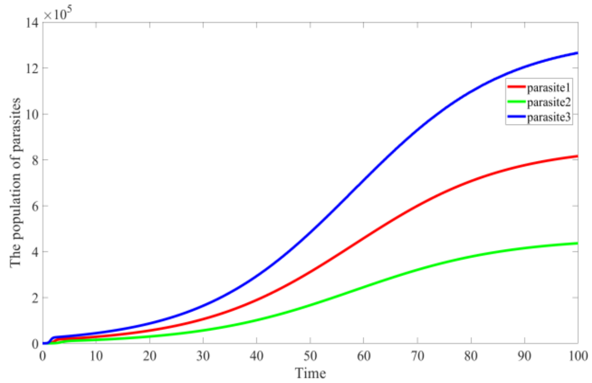
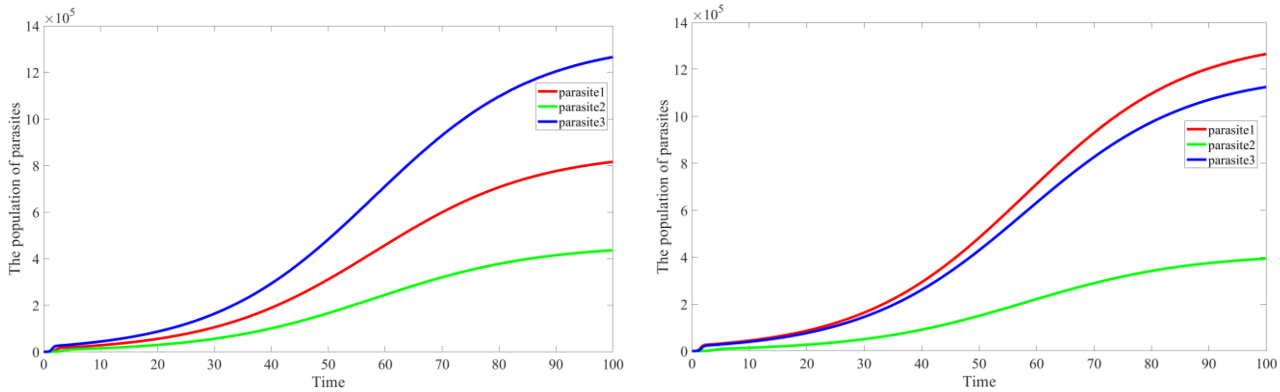


Fig 5. Changes in the population size of parasites when the gender ratio is stable.

From the Fig. 4 and Fig. 5, the gender ratio does not change, which means that there are more females and stronger predatory abilities, so the number of parasite 1 decreases. Due to the decrease in males and weakened competitiveness, the number of parasite 2 has increased. Due to the increase in the population of lampreys, more hosts can parasitize, increasing the number of parasites 3.



(a) constant gender ratio (b) male ratio rises

Fig 6. Comparison of parasite numbers when gender ratio changes and remains unchanged.

We set the initial number of female and male lampreys to 100, and the number of three types of parasites to 50.

As shown in Fig. 6, by comparison, when the male ratio of the lamprey population rises: the number of parasites in predatory relationships has increased from 8.1×10^5 to 12.8×10^5. The number of parasites in competitive relationships has decreased from 4.3×10^5 to 4×10^5. The number of parasites in parasitic relationships has decreased from 13×10^5 to 11.5×10^5.

In conclusion, after the male ratio rises, the reproductive rate and population size of the lamprey population will decrease, but at the same time, the male ratio will increase. Therefore, considering both factors, the male population will remain the same. This result leads to less fluctuation in the number of parasites in competitive relationships. The number of females has decreased, so the number of parasites in predatory relationships has significantly increased. For parasitic parasites, their number varies with the total population of lampreys, so it only decreases slightly.

5. Summary

Through this paper, we have gained a deeper understanding of the effects of adaptive sex ratio variation on the ecosystem of lampreys. We found that variation in the sex ratio of lampreys significantly affects population size and periodicity, while the ecosystem is more stable within a specific sex ratio range. In addition, as the proportion of males increased, prey populations increased, with less impact on competitors, and parasites decreased slightly. Taken together, adaptive sex ratio variation not only affects lampreys' population dynamics, but also has important implications for ecosystem stability and interspecific relationships. These findings provide important references for future studies and help us to better understand the effects of sex ratio variation on ecosystems for better conservation and management of ecosystems.

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