

一类具有Holling-II型功能反应的食饵带恐惧效应与捕食者非线性收获的捕食者-食饵模型的动力学性态

李 立

西北师范大学数学与统计学院, 甘肃 兰州

收稿日期: 2024年6月3日; 录用日期: 2024年6月26日; 发布日期: 2024年7月4日

摘 要

本文研究了具有 Holling-II 型功能反应的捕食者-食饵模型的恐惧效应和对捕食者种群的非线性收获。对捕食者种群的恐惧增强了食饵种群的生存率, 同时也大大减少了食饵种群的繁衍。对捕食者种群的捕获不仅可以获取经济收益, 还可以调节捕食者与食饵的数量关系。文中研究了所有的生物可行平衡点并分析了可行平衡点的稳定时的模型参数。分析上, 我们选择以捕食者种群的转化率为分支参数。模型系统经历了跨临界分支, 鞍结分支和 Hopf 分支。考虑捕食者和食饵种群在时空内的扩散效应, 接着研究了正平衡点的局部稳定性, 正平衡点和分支周期解的 Turing 不稳定性, Hopf 分支的方向和分支周期解的稳定性。

关键词

Holling-II 型功能反应, 平衡点, 稳定性, Hopf 分支, 恐惧效应, Turing 不稳定性

Dynamics of a Class of Prey-Predator Interaction Model with Holling Type-II Functional Response Incorporating the Effect of Fear on Prey and Non-Linear Predator Harvest

Li Li

College of Mathematics and Statistics, Northwest Normal University, Lanzhou Gansu

Received: Jun. 3rd, 2024; accepted: Jun. 26th, 2024; published: Jul. 4th, 2024

Abstract

In this paper, we investigate the effects of fear effect and nonlinear predator harvest in predator-prey interaction models with Holling-II type functional response. Fear of the predator population increases the survival rate of the prey population and also greatly reduces the birth rate. The capture of the predator population can not only obtain economic benefits, but also regulate the quantitative relationship between predator and prey. In this paper, all viable equilibrium points are studied and the model parameters of stability of stability of viable equilibrium points are analyzed. In analysis, we have established that the conversion rate of predator population is the branch parameter and the model system undergoes transcritical branch, saddle-node branch and Hopf branch. Considering the diffusion effect of predator and prey population in space and time, we study the local stability of the positive equilibrium point, the positive equilibrium point and the Turing of the branch periodic solution instability, the direction of the Hopf branch and stability of the periodic solution of the branch.

Keywords

Holling-II Type Functional Response, Equilibrium, Stability, Hopf Branch, Fear Effect, Turing Instability

Copyright © 2024 by author(s) and Hans Publishers Inc.

This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

1. 引言

自经典的 Lotka-volterra 模型提出以来,运用数学方法对生态系统的动力学行为的研究已经有了很长的历史.随着研究的深入发展,研究人员提出更合理,更实用的捕食者-食饵模型.受多种因素的影响,捕食者与食饵相互作用可能表现出更复杂的动力学行为,即使在生物学意义上对模型进行细微的调整,捕食者-食饵相互作用的动力学行为也会发生较大的变化.

C.S.Holling 在对捕食者-食饵动力学研究中首次引入“功能反应”,不仅用于描述食饵种群密度变化时捕食者消耗食饵速度的变化 [1-3], 还考虑了食饵的种群密度,捕食者的捕获能力,猎杀处理效率以及消化时间等关键因素.

假设在没有捕食者存在的情况下,食饵种群数量按逻辑增长,此时食饵的逻辑增长有三部分:食饵种群的出生率,死亡率以及由于食饵种群的种内竞争导致的数量减少,因此食饵种群可用下式表示 [4]:

$$\frac{dx}{dt} = rx - dx - ax^2 \quad (1.1)$$

$x(t)$ 是 t 时刻食饵的种群密度, r 是食饵种群的内禀增长率, d 代表食饵种群的死亡率, a 代表食饵的种内竞争导致的数量减少.对(1.1)式考虑具有 Holling-II 型功能反应的捕食者-食饵模型 [5-9],得(1.2)式如下:

$$\frac{dx}{dt} = rx - dx - ax^2 - \frac{pxy}{1+qx} \quad (1.2)$$

$$\frac{dy}{dt} = \frac{cpxy}{1+qx} - my \quad (1.3)$$

$y(t)$ 是 t 时刻捕食者的种群密度, p, q 代表最大捕食率和处理时间, c 代表由食饵到捕食者的转化率.由于捕食者种群的存在会对食饵种群数量的增长产生负影响,我们将这种负影响称为恐惧因子,记作 $\psi(k, y) = \frac{1}{1+ky}$.将恐惧因子乘以食饵的出生项作为新的食饵增长率,其中 k 是食饵对捕食者的恐惧水平 [10-12], $\psi(k, y)$ 满足:

1. $\psi(0, y) = 1$; 如果食饵没有反捕食行为, 那么食饵的出生率就不会降低.
2. $\psi(k, 0) = 1$; 如果食饵的数量为零, 那么食饵的出生率也不会降低.
3. $\lim_{k \rightarrow \infty} \psi(k, y) = 0$; 如果食饵的反捕食行为非常大, 那么食饵的出生率最终变为 0.
4. $\lim_{y \rightarrow \infty} \psi(k, y) = 0$; 如果捕食者种群数量非常大, 那么由于反捕食行为, 食饵的出生率最终变为 0.
5. $\frac{\partial \psi(k, y)}{\partial k} < 0$; 随着反捕食行为的增加, 食饵种群的增长率下降.

6. $\frac{\partial \psi(k, y)}{\partial y} < 0$; 食饵种群的增长率随捕食者种群密度的增加而减少.

在捕食者-食饵模型中,生物资源可以被收获和出售,以实现经济效益.基于此本文在捕食者项引入收获项,使模型从生态和经济的角度更加符合实际.主要有三种不同的收获函数.第一种是恒定收获,即单位时间内收获恒定数量的捕食者个体.第二种是线性收获,单位时间内收获的个体数量与当时存在的个体数量成正比.最后一种是非线性收获也称作 Michaelis-Menten 型收获 [13, 14], 记作 $H(y) = \frac{nEy}{r_1E + r_2y}$, 其中 E 是人为因素的影响, r_1 和 r_2 是适当的常数.

$$\begin{cases} \frac{dx}{dt} = \frac{rx}{1+ky} - dx - ax^2 - \frac{pxy}{1+qx} = f_1(x, y) \\ \frac{dy}{dt} = \frac{cpxy}{1+qx} - my - \frac{nEy}{r_1E + r_2y} = f_2(x, y) \end{cases} \quad (1.4)$$

对模型(1.4)做无量纲变换:

$$\tau = rt, \quad u = \frac{a}{r}x, \quad v = \frac{y}{p}, \quad d^* = \frac{d}{r}, \quad q^* = \frac{qr}{a}, \quad k^* = kp, \quad c^* = \frac{cp}{a}m^* = \frac{m}{r}, \quad h = \frac{r_1E}{r_2}, \quad n^* = \frac{nE}{r_2r}.$$

将 $\tau, d^*, q^*, k^*, c^*, m^*, n^*$ 重新记为 t, d, q, k, c, m, n . 模型(1.4)变为

$$\begin{cases} \frac{du}{dt} = \frac{u}{1+kv} - du - u^2 - \frac{uv}{1+qu} = f_1(u, v) \\ \frac{dv}{dt} = \frac{cuv}{1+qu} - mv - \frac{nv}{h+v} = f_2(u, v) \end{cases} \quad (1.5)$$

在自然界中,捕食者和食饵在时间空间上都不是固定不变的,它们的分布受环境,食物供应,季节等多种因素的影响而不断变化.因此将物种的扩散,传播引入捕食者-食饵模型能更真实的反应自然环境中的情景,本文将考虑齐次 Neumann 边界条件下的捕食者-食饵模型.

$$\begin{cases} \frac{\partial u}{\partial t} - D_1 \frac{\partial^2 u}{\partial s^2} = \frac{u}{1+kv} - du - u^2 - \frac{uv}{1+qu}, s \in (0, \pi), t > 0 \\ \frac{\partial v}{\partial t} - D_2 \frac{\partial^2 v}{\partial s^2} = \frac{cuv}{1+qu} - mv - \frac{nv}{h+v}, s \in (0, \pi), t > 0 \\ u_s(0, t) = u_s(\pi, t), t > 0 \\ v_s(0, t) = v_s(\pi, t), t > 0 \end{cases} \quad (1.6)$$

2. 平衡点的存在性和稳定性

2.1. 平衡点的存在性

对于系统(1.5):

(i) 系统总存在平凡平衡点 $E_0 = (0, 0)$;

(ii) 当 $1 > d$ 时, 轴向平衡点 $E_1 = (1 - d, 0)$ 存在;

(iii) 内部平衡点 $E_* = (u^*, v^*)$, 此处 $v^* = \frac{n + mh + (nq + mhq - ch)u}{u(c - mq) - m}$, u 是方程

$$A_1 u^4 + A_2 u^3 + A_3 u^2 + A_4 u + A_5 = 0$$

的正根.

令 $a_* = c - mq$, $b_* = n + mh$, $c_* = nq + mhq - ch$. $A_1 = a_*^2 q + a_* c_* k q$,
 $A_2 = a_*^2 + a_* c_* k + a_* b_* k q + a_*^2 d q + 2 a_* c_* k d q - 2 a_* m q - c_* k m q - a_*^2 q$,
 $A_3 = a_* b_* k + a_*^2 d + a_* c_* k d + m^2 q + a_* m q - 2 m a_* - b_* k m q - a_* d m q - k c_* d m q - k c_* - k a_* b_* q$,
 $A_4 = k b_* + k b_* c_* + a_* b_* + a_* m d + k c_* m d + m^2 + 2 a_* m - m^2 q$,
 $A_5 = k b_* m - 2 m^2 + m b_* - k b_*^2$.

2.2. 平衡点的局部稳定性

系统(1.5)在 (u, v) 处的 Jacobian 矩阵如下:

$$J_E = \begin{pmatrix} f_{1u} & f_{1v} \\ f_{2u} & f_{2v} \end{pmatrix}$$

此处 $f_{1u} = \frac{1}{1 + kv} - d - 2u - \frac{v}{1 + qu} + \frac{quv}{(1 + qu)^2}$, $f_{1v} = -\frac{ku}{(1 + kv)^2} - \frac{u}{1 + qu}$.

$$f_{2u} = \frac{cv}{(1 + qu)^2}, \quad f_{2v} = \frac{cu}{1 + qu} - m - \frac{n}{h + v} + \frac{nv}{(h + v)^2}.$$

定理 1 平凡平衡点 $E_0 = (0, 0)$ 是一个鞍点, 是无条件不稳定的.

证明 系统(1.5)在平衡点 E_0 处的 Jacobian 矩阵为

$$\mathbf{J}_{E_0} = \begin{pmatrix} 1 - d & 0 \\ 0 & -m - n \end{pmatrix}.$$

矩阵 $\mathbf{J}_{E_0}$ 的特征值为 $\lambda_1 = 1 - d > 0$, $\lambda_2 = -m - n < 0$. 因此, 平凡平衡点 E_0 是不稳定的.

定理 2 如果 $c < c^*$ 时, 轴向平衡点 $E_1 = (1 - d, 0)$ 是稳定的, $c > c^*$ 时, 轴向平衡点 $E_1 = (1 - d, 0)$ 是不稳定的, 此处 $c^* = \frac{m(1 + q - d)}{1 - d} + \frac{n(1 + q(1 - d))}{(1 - d)(h + 1 - d)}$.

证明 系统(1.5)在平衡点 E_1 处的 Jacobian 矩阵为

$$J_{E_1} = \begin{pmatrix} -(1 - d) & -\frac{(1 - d)(k(1 + q(1 - d)) + 1)}{1 + q(1 - d)} \\ 0 & (c - c^*) \frac{1 - d}{1 + q(1 - d)} \end{pmatrix}.$$

矩阵 J_{E_1} 的特征值为 $\lambda_1 = -(1-d) < 0$, $\lambda_2 = (c-c^*)\frac{1-d}{1+q(1-d)}$, 当 $c < c^*$ 时 $\lambda_2 < 0$, 所以轴向平衡点 $E_1 = (1-d, 0)$ 是渐近稳定的.

定理 3 如果 $C_1 > 0$, $C_2 > 0$ 时, 内部平衡点 $E_* = (u^*, v^*)$ 是稳定的; 否则, $E_* = (u^*, v^*)$ 是不稳定的.

证明 系统(1.5)在平衡点 $E_*(u^*, v^*)$ 处的 Jacobian 矩阵为:

$$J_{E_*} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

$$a_{11} = \frac{1}{1+kv^*} - d - 2u^* - \frac{v^*}{1+qu^*} + \frac{qu^*v^*}{(1+qu^*)^2}, \quad a_{12} = -\frac{ku^*}{(1+kv^*)^2} - \frac{u^*}{1+qu^*}, \quad a_{21} = \frac{cv^*}{(1+qu^*)^2},$$

$$a_{22} = \frac{cu^*}{1+qu^*} - m - \frac{n}{h+v^*} + \frac{nv^*}{(h+v^*)^2}.$$

J_{E_*} 的特征方程是

$$\lambda^2 + C_1\lambda + C_2 = 0 \quad (2.1)$$

此处 $C_1 = -(a_{11} + a_{22})$, $C_2 = a_{11}a_{22} - a_{12}a_{21}$.

当 $C_1 > 0$, $C_2 > 0$ 时, 特征方程(2.1)的根都有负的实部部分, 所以内平衡点 $E_*(u^*, v^*)$ 是局部渐近稳定的. 如果 $C_2 < 0$, 则特征方程(2.1) 的根具有相反的符号, 所以 $E_*(u^*, v^*)$ 是鞍点.

3. 分支分析

3.1. 跨临界分支

定理 4 当 $c = c^*$ 时, 系统(1.5)在轴向平衡点 $E_1(1-d, 0)$ 处发生跨临界分支.

证明 当 $c = c^*$, 在点 $E_1(1-d, 0)$ 处的 Jacobian 矩阵的特征值为 $-(1-d)$ 和 0. 由于两个特征根, 一个为负另一个为 0, 因此无法得到稳定与否的结论. 令 $J(E_1)$ 和 $J(E_1)^T$ 对应特征值的零特征转化因子为 $V = (0, 1)^T$ 和 $G = (0, 1)^T$. 由跨临界分支的 Sotomayor 定理 [15] 可得:

$$(i) \quad W^T F_c(E_1) = 0,$$

$$(ii) \quad W^T [DF_c(E_1)G] = \frac{1-d}{1+q(1-d)} \neq 0,$$

$$(iii) \quad W^T [D^2 F_c(E_1)(G, G)] = \frac{2n}{h^2} \neq 0.$$

$E_1(1-d, 0)$ 满足跨临界分支条件, 故系统(1.5)在 $E_1(1-d, 0)$ 处发生跨临界分支.

3.2. 鞍结分支

定理 5 如果满足 $2a_{21}a_{22}^2e_{12} + a_{12}a_{22}^2e_{21} + a_{12}a_{21}^2e_{23} \neq a_{22}^3e_{11} + a_{21}^2a_{22}e_{13} + 2a_{12}a_{21}a_{22}e_{22}$, 则 $c = c^{[SN]}$ 时, 系统(1.5)在内部平衡点 $E_*(u^*, v^*)$ 处发生鞍结分支.

证明 在 $c = c^{[SN]}$ 时, 满足 J_{E_*} 的一个特征值为 0, 根据 Sotomayor 定理, 考虑如下方程 $F(U, c) = [f_1(u, c), f_2(u, c)]^\tau$, 此处 $U = (u, v)$.

$$DF(U, c)|_{E_*} = J_{E_*} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

令 $G = (G_{11}, G_{12})^\tau, W = (W_{11}, W_{12})^\tau$.

其中 $G_{11} = -a_{22}, G_{12} = a_{21}, W_{11} = -a_{22}, W_{12} = a_{12}$.

$$(i) W^\tau F_c(E_*) = a_{12} \frac{u^* v^*}{1 + qu^*} \neq 0,$$

$$(ii) W^\tau [D^2 F_c(E_*)(G, G)] = (-a_{22}, a_{12}) \begin{pmatrix} a_{22}^2 e_{11} - 2a_{21} a_{22} e_{12} + a_{21}^2 e_{13} \\ a_{22}^2 e_{21} - 2a_{21} a_{22} e_{22} + a_{21}^2 e_{23} \end{pmatrix} \neq 0.$$

$$\begin{aligned} & \text{可得 } 2a_{21}a_{22}^2e_{12} + a_{12}a_{22}^2e_{21} + a_{12}a_{21}^2e_{23} \neq a_{22}^3e_{11} + a_{21}^2a_{22}e_{13} + 2a_{12}a_{21}a_{22}e_{22}. \\ e_{11} &= -2 + \frac{2qv^*}{(1+qu^*)^2} - \frac{2q^2u^*v^*}{(1+qu^*)^3}, \quad e_{12} = -\frac{k}{(1+kv)^2} - \frac{1}{1+qu} + \frac{qu}{(1+qu)^2}. \\ e_{13} &= \frac{2k^2u^*}{(1+kv^*)^3}, \quad e_{21} = \frac{cqv^*}{(1+qu^*)^2} - \frac{cq^2u^*v^*}{(1+qu^*)^3}, \quad e_{22} = \frac{c}{1+qu^*} - \frac{cqu^*}{(1+qu^*)^2}, \\ e_{23} &= \frac{2n}{(h+v)^2} - \frac{2nv^*}{(h+v)^3}. \end{aligned}$$

3.3. Hopf分支

讨论内部平衡点 $E_*(u^*, v^*)$ 处的Hopf分支, 并且将捕食者的转换率作为分支参数用来验证横截条件.

定理 6 在 $c = c^{[HB]}$ 处, 如果 $C_1 = 0, C_2 > 0$ 并且 $C'_1 | c = c^{[HB]} \neq 0$, 则系统(1.5)会在点 $E_*(u^*, v^*)$ 处发生 Hopf 分支.

证明 假设特征方程(2.1)对于参数 c 的某个临界值在内部平衡点 $E_*(u^*, v^*)$ 处有一对纯虚根, 则 $C_1 = 0, C_2 > 0$.

特征方程(2.1)可化简得.

$$\lambda^2 + C_2 = 0$$

解上式可得, 在 $c = c^{[HB]}$ 处 $\lambda_{1,2} = \pm\sqrt{C_2}$. 取一个非常小的扰动 $\varepsilon > 0$, 存在一个邻域 $(c^{[HB]} - \varepsilon, c^{[HB]} + \varepsilon)$ 使得对任何 $c \in (c^{[HB]} - \varepsilon, c^{[HB]} + \varepsilon)$ 特征方程的根可写作 $\lambda_{1,2} = \omega_1(c) + i\omega_2(c)$, 把 $\lambda_1(c)$ 带入(2.1)式, 并分离实部与虚部.

$$\begin{cases} \omega_1^2(c) - \omega_2^2(c) + C_1\omega_1(c) + C_2 = 0 \\ 2\omega_1(c)\omega_2(c) + C_1\omega_2(c) = 0 \end{cases} \quad (3.1)$$

对(3.1)式两边同时求微分

$$\begin{cases} 2\omega_1(c)\omega'_1(c) + C_1(c)\omega'_1(c) - 2\omega_2(c)\omega'_2(c) + C'_1(c)\omega_1(c) + C'_2 = 0 \\ 2\omega'_1(c)\omega_2(c) + (2\omega_1(c) + C_1(c))\omega'_2(c) + C'_1(c)\omega_2(c) = 0 \end{cases} \quad (3.2)$$

解得:

$$\omega'_1(c) = -\frac{2\omega_2^2(c)C'_1(c) + \omega_1(c)(2C'_2(c) + 2\omega_1(c)C_1(c) + C_1(c)C'_1(c)) + C_1(c)C'_2(c)}{4\omega_2^2(c) + (2\omega_1(c) + C_1(c))^2}$$

在临界值 $c = c^{[HB]}$ 处 $C_1(c^{[HB]}) = 0, \omega_1(c^{[HB]}) = 0, \omega_2(c^{[HB]}) = \sqrt{C_2}$.

解(3.2)式得:

$$\frac{d\omega_1(r)}{dc} \big|_{c=c^{[HB]}} = -\frac{1}{2}C'_1(c) \big|_{c=c^{[HB]}} \neq 0.$$

综上 Hopf 分支的横截性条件得以验证.

3.4. Hopf 分支的稳定性

本节采用中心流形定理求解 Hopf 分支的方向,首先对系统(1.5)做 $u = u' + u_1, v = v' + v_1$ 变换并展开.

$$\begin{aligned} \frac{du}{dt} &= a_{11}u + a_{12}v + a_{13}u^2 + a_{14}uv + a_{15}v^2 + a_{16}u^3 + a_{17}u^2v + a_{18}uv^2 + a_{19}v^3 + \dots, \\ \frac{dv}{dt} &= a_{21}u + a_{22}v + a_{23}u^2 + a_{24}uv + a_{25}v^2 + a_{26}u^3 + a_{27}u^2v + a_{28}uv^2 + a_{29}v^3 + \dots, \end{aligned}$$

$$\begin{pmatrix} \frac{du}{dt} \\ \frac{dv}{dt} \end{pmatrix} = J_{E_*} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} g_1(u, v) \\ g_2(u, v) \end{pmatrix}. \quad (3.3)$$

其中

$$\begin{aligned} g_1(u, v) &= a_{13}u^2 + a_{14}uv + a_{15}v^2 + a_{16}u^3 + a_{17}u^2v + a_{18}uv^2 + a_{19}v^3 + \dots, \\ g_2(u, v) &= a_{23}u^2 + a_{24}uv + a_{25}v^2 + a_{26}u^3 + a_{27}u^2v + a_{28}uv^2 + a_{29}v^3 + \dots, \end{aligned}$$

$$\begin{aligned} a_{13} &= -1 + \frac{qv}{(1+qu)^2} - \frac{q^2uv}{(1+qu)^3}, a_{14} = -\frac{k}{(1+kv)^2} - \frac{1}{(1+qu)} + \frac{qu}{(1+qu)^2}, \\ a_{15} &= \frac{k^2u}{(1+kv)^3}, a_{16} = -\frac{q^2v}{(1+qu)^3} + \frac{q^3uv}{(1+qu)^4}, a_{17} = \frac{q}{(1+qu)^2} - \frac{q^2u}{(1+qu)^3}, \\ a_{18} &= \frac{k^2}{(1+kv)^3}, a_{19} = -\frac{k^3u}{(1+kv)^4}, a_{23} = -\frac{cqv}{(1+qu)^2} + \frac{cq^2uv}{(1+qu)^3}, a_{24} = \frac{c}{(1+qu)} - \frac{cqu}{(1+qu)^2}, \\ a_{25} &= \frac{n}{(h+v)^2} - \frac{nv}{(h+v)^3}, a_{26} = \frac{cq^2v}{(1+qu)^3} - \frac{q^3uv}{(1+qu)^4}, a_{27} = -\frac{cq}{(1+qu)^2} + \frac{cq^2u}{(1+qu)^3}, \\ a_{28} &= 0, a_{29} = \frac{n}{(h+v)^3} + \frac{nv}{(h+v)^4}. \end{aligned}$$

系统(3.3)不考虑4阶及以上部分时可重写为:

$$\dot{U} = J_{E_*} U + \Lambda(U) \quad (3.4)$$

$$\text{此处 } J_{E_*} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad \Lambda(U) = \begin{pmatrix} g_1(u, v) \\ g_2(u, v) \end{pmatrix}.$$

在 $c = c^{[HB]}$ 处的 Jacobian 矩阵具有纯虚根,其特征值 $i\omega_2$ 对应的特征向量为 $\bar{x} = (a_{12}, i\omega_2 - a_{11})^\tau$.

$$P = (\underline{Re}(\bar{X}) + \underline{Im}(\bar{X})) = \begin{pmatrix} a_{11} & 0 \\ -a_{11} & -\omega_2 \end{pmatrix}.$$

通过变换 $U = PX, U = (u, v)^\tau, X = (x, y)^\tau$, 系统(3.4)变为:

$$\dot{X} = (P^{-1}J(E_*)P)X + P^{-1}\Lambda(PX)$$

将此式重写为:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} 0 & -\omega_2 \\ \frac{a_{11}a_{22} - a_{21}a_{12}}{\omega_2} & a_{11} + a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} g_1(x, y) \\ g_2(x, y) \end{pmatrix}. \quad (3.5)$$

$$g_1(x, y) = \frac{1}{a_{12}}G_1(x, y), \quad g_2(x, y) = -\frac{1}{\omega_2 a_{12}}(a_{11}G_1(x, y) + a_{12}G_2(x, y)).$$

$$\begin{aligned} G_1(x, y) = & (a_{12}a_{13} - a_{11}a_{12}a_{14} + a_{11}^2a_{15})x^2 + (2a_{11}a_{15}\omega_2 - a_{12}a_{14}\omega_2)xy + a_{15}\omega_2^2y^2 \\ & + (a_{12}^3a_{16} - a_{11}a_{12}^2a_{17} + a_{11}^2a_{12}a_{18} - a_{11}^3a_{19})x^3 + (2a_{11}a_{12}a_{18}\omega_2 - a_{12}^2a_{17}\omega_2 \\ & - 3a_{11}^2\omega_2 - 3a_{11}^2a_{19}\omega_2)x^2y + (a_{12}a_{18}\omega_2^2 - 3a_{11}a_{19}\omega_2^2)xy^2 - a_{19}\omega_2^3y^3. \end{aligned}$$

$$\begin{aligned} G_2(x, y) = & (a_{11}a_{23} - a_{11}a_{12}a_{24} + a_{11}^2a_{25})x^2 + (2a_{11}a_{25}\omega_2 - a_{12}a_{24}\omega_2)xy + a_{25}\omega_2^2y^2 \\ & + (a_{12}^3a_{26} - a_{11}a_{12}^2a_{27} - a_{11}^3a_{29})x^3 - (a_{12}^2a_{27}\omega_2 + 3a_{11}^2\omega_2 + 3a_{11}^2a_{19}\omega_2)x^2y \\ & - 3a_{11}a_{29}\omega_2^2xy^2 - a_{29}\omega_2^3y^3. \end{aligned}$$

计算第一 Lyapunov 系数,并根据系数的符号来判断周其轨道的稳定性和不稳定性.第一 Lyapunov 系数的求解如下:

$$\begin{aligned} \Theta = & \frac{1}{16}\{g_{1xxx} + g_{1xyy} + g_{2xxy} + g_{2yyy}\} \\ & + \frac{1}{16\omega_2}\{g_{1xy}(g_{1xx} + g_{1yy}) - g_{2xy}(g_{2xx} + g_{2yy}) - g_{1xx}g_{2xx} + g_{1yy}g_{2yy}\}. \end{aligned}$$

如果 $\Theta < 0$ 则系统(1.5)具有稳定的极限周期环并且 Hopf 分支是超临界的;如果 $\Theta > 0$ 则系统(1.5)不具有稳定的极限周期环并且 Hopf 分支是亚临界的. 当 $\Theta = 0$ 系统(1.5)在内部平衡点存在广义 Hopf 分支.

4. 反应扩散系统

本节讨论一维 $(0, \pi)$ 的 Neumann 边界条件下的 PDE 模型:

$$\begin{cases} \frac{\partial u}{\partial t} - D_1 \frac{\partial^2 u}{\partial s^2} = \frac{1}{1+kv} - du - u^2 - \frac{uv}{1+qu}, s \in (0, \pi), t > 0 \\ \frac{\partial v}{\partial t} - D_2 \frac{\partial^2 v}{\partial s^2} = \frac{cuv}{1+qu} - mv - \frac{nv}{h+v}, s \in (0, \pi), t > 0 \\ \frac{\partial u}{\partial s} = \frac{\partial v}{\partial s} = 0, s \in \partial(0, \pi), t > 0 \\ x_s(0, t) = x_s(\pi, t), y_s(0, t) = y_s(\pi, t), t > 0 \end{cases} \quad (4.1)$$

4.1. 正平衡点的 Turing 不稳定性

令 $0 = \mu_1 < \mu_2 < \mu_3 < \cdots < \mu_n \rightarrow \infty$ 是椭圆算子 $-\Delta$ 在 Ω 上相应于齐次 Neumann 边界条件的所有特征值. $\Gamma(\mu_n)$ 是相应 μ_n 在 $H^1(\Omega)$ 中的特征空间. 设 Υ 是 $(C^1(\bar{\Omega}))^2$ 在 $(H^1(\Omega))^2$ 中的闭包, $\{\phi_{ns} : s = 1, 2, \cdots, \dim \Gamma(\mu_n)\}$ 是 $\Gamma(\mu_n)$ 的标准正交基. 并定义 $\Upsilon_{ns} = \{\mathbf{c}\phi_{ns} : \mathbf{c} \in \mathbb{R}^2\}$, 则:

$$\Upsilon = \bigoplus_{n=1}^{+\infty} \Upsilon_n, \quad \Upsilon_n = \bigoplus_{s=1}^{\dim \Gamma(\mu_n)} \Upsilon_{ns}.$$

定理 7 假设定理3成立, 且 $d_1 \leq -\frac{a_{11}}{a_{22}}d_2$ 则模型(4.1)的正平衡点 $E_*(u^*, v^*)$ 是局部一致渐近稳定的.

证明 令 $D_* = \text{diag}(d_1, d_2)$, $E = (u, v)^\tau$, $L = D_*\Delta + J_{E_*}$, 则(4.1)在平衡点 E_* 处的线性化系统为

$$E_t = LE. \quad (4.2)$$

对于每一个 $n \geq 1$, 算子 L 的特征值是矩阵 $-\mu_n D_* + J_{E_*}$ 的特征值, $-\mu_n D_* + J_{E_*}$ 的特征方程为:

$$g_n(\lambda) \triangleq |\lambda I + \mu_n D_* - J_{E_*}(\bar{E})| = \lambda^2 + M_n \lambda + N_n,$$

其中

$$M_n = (d_1 + d_2)\mu_n + C_1, \quad N_n = d_1 d_2 \mu_n^2 - (a_{11} d_2 + a_{22} d_1)\mu_n + C_2.$$

定理3成立意味着 $a_{11} < 0$, 且当 $d_1 \leq -\frac{a_{11}}{a_{22}}d_2$ 时, $M_n > 0$, $N_n > 0$. 因此, $g_n(\lambda) = 0$ 的两个根 $\lambda_{n,1}$ 和 $\lambda_{n,2}$ 均有负实部.

下面证明存在正常数 $\bar{\delta}$ 使得

$$\text{Re}\{\lambda_{n,1}\}, \text{Re}\{\lambda_{n,2}\} \leq -\bar{\delta}, \quad \forall n \geq 1. \quad (4.3)$$

令 $\lambda = \mu_n \varrho$, 则

$$g_n(\lambda) = \mu_n^2 \varrho^2 + M_n \mu_n \varrho + N_n \triangleq \bar{g}_n(\varrho).$$

由于 $n \rightarrow \infty$ 时 $\mu_n \rightarrow \infty$, 所以

$$\lim_{n \rightarrow \infty} \frac{\bar{g}_n(\varrho)}{\mu_n^2} = \varrho^2 + (d_1 + d_2)\varrho + d_1 d_2 \triangleq \bar{g}(\varrho).$$

注意到方程 $\bar{g}_n(\varrho) = 0$ 的两个根均有负实部: $-d_1, -d_2$. 由连续性, 存在 n_0 使得对所有的 $n \geq n_0$, 方程 $\bar{g}_n(\varrho) = 0$ 的两根 $\varrho_{n,1}, \varrho_{n,2}$ 满足:

$$\operatorname{Re}\{\varrho_{n,1}\}, \operatorname{Re}\{\varrho_{n,2}\} \leq -\frac{\hat{d}}{2}, \quad \hat{d} = \min\{d_1, d_2\}.$$

故有 $\operatorname{Re}\{\lambda_{n,1}\}, \operatorname{Re}\{\lambda_{n,2}\} \leq -\frac{\hat{d}}{2}, \forall n \geq n_0$.

取

$$\max_{1 \leq n \leq n_0} \{\operatorname{Re}\{\lambda_{n,1}\}, \operatorname{Re}\{\lambda_{n,2}\}\} = -\varpi,$$

则 $\varpi > 0$. 从而(4.3)对 $\delta = \min\{\varpi, \frac{\hat{d}}{2}\}$ 成立. 故 $E_*(u^*, v^*)$ 局部一致渐近稳定.

算子 $\phi \rightarrow \phi''$ 在 (π, t) 边界上满足 $\phi'(0) = \phi'(\pi) = 0$, 且算子有特征值 $\mu_0 = 0, \mu_k = k^2, k = 1, 2, 3, \dots$, 其标准化特征方程为 $\phi_0(s) = \sqrt{\frac{1}{\pi}}, \phi_k(s) = \sqrt{\frac{2}{\pi}} \cos(ks)$. 系统(4.1)在内部平衡点 $E_*(u^*, v^*)$ 处有下列形式:

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = L \begin{pmatrix} u \\ v \end{pmatrix} = D \begin{pmatrix} \Delta u \\ \Delta v \end{pmatrix} + J_{E_*} \begin{pmatrix} u \\ v \end{pmatrix}, \quad (4.4)$$

J_{E_*} 是在内部平衡点 $E_*(u^*, v^*)$ 处的 Jacobian 矩阵

$$D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$$

L 是一个关于 $D_L = X_C = X \oplus iX = \{x_1 + ix_2, x_1, x_2 \in X\}$ 的线性算子, 此处 $X := \{(x, y) \in H^2[(0, \pi)] \times H^2[(0, \pi)] : x'(0) = x'(\pi) = y'(0) = y'(\pi)\}$. 是一个实值 Sobolev 空间.

考虑算子 L 的特征方程

$$L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \mu \begin{pmatrix} \phi \\ \psi \end{pmatrix}$$

令 $(\phi(s), \psi(s))^T$ 是与算子 L 对应的特征值, 则 μ 的特征方程为

$$\begin{pmatrix} \phi \\ \psi \end{pmatrix} = \sum_{n=1}^{+\infty} \begin{pmatrix} a_k \\ b_k \end{pmatrix} \cos(ks)$$

此处 a_k, b_k 是系数.

记

$$J_k = J_{E_*} - k^2 D = \begin{pmatrix} a_{11} - k^2 D_1 & -a_{12} \\ -a_{21} & a_{22} - k^2 D_2 \end{pmatrix}.$$

算子 L 的特征矩阵由 J_k 的特征值得出, J_k 的特征方程为

$$Z_k(\lambda) = \lambda^2 - T_k \lambda + D_k = 0. \quad (4.5)$$

此处

$$T_k = a_{11} + a_{22} - k^2(D_1 + D_2), \quad D_k = (a_{11} - k^2 D_1)(a_{22} - k^2 D_2) - a_{12} a_{21}.$$

由定理3知,当 $C_1 > 0, C_2 > 0$ 时,内部平衡点 $E_*(u^*, v^*)$ 渐近稳定.

通过分析(4.5)式根的分布可得. $E_*(u^*, v^*)$ 是系统(1.5)的局部渐近稳定平衡点,如果 $T_k < 0, D_k > 0$ 时 $E_*(u^*, v^*)$ 是系统(4.1)的局部渐近稳定解.

由 $T_k < 0, D_k > 0$ 得:

$$H_1 : D_2 \leq -\frac{a_{22}}{a_{11}} D_1$$

$$H_2 : D_2 \geq a_{22}$$

证明 首先, $T_k := a_{11} + a_{22} - k^2(D_1 + D_2) = -C_1 - k^2(D_1 + D_2) \leq 0$, 是显然的.

接下来 $D_k = (a_{11} - k^2 D_1)(a_{22} - k^2 D_2) - a_{12} a_{21} = D_1 D_2 k^4 - k^2(a_{22} D_1 + a_{11} D_2) + C_2 \geq 0$, 则 $a_{22} D_1 + a_{11} D_2 \leq 0$ 可得 $D_1 \geq -\frac{a_{11}}{a_{22}} D_2$. 同时, $T_k = (a_{11} - k^2 D_1)(a_{22} - k^2 D_2) - a_{12} a_{21} \geq 0$ 时要满足 $a_{22} - k^2 D_2 \leq 0$, 也就是 $a_{22} \leq k^2 D_2$ 进一步得 $a_{22} \leq D_2$.

定理 8 如果 $C_1 > 0, C_2 > 0$. 则存在一个不稳定区域.

$$U = \{(D_1, D_2) : a_{22} \geq D_2 \geq -\frac{a_{22}}{a_{11}} D_1; D_1, D_2 > 0\}$$

对任意 $(D_1, D_2) \in U$, 都有 $E_*(u^*, v^*)$ 是 Turing 不稳定的.

4.2. 空间其次周期解的稳定性

在 $c = c^{[HB]}$ 附近讨论空间其次周期解的稳定性,常微系统(1.5)与偏微系统(4.1)在同一点的稳定性有可能相同也可能不同.如果 $\phi(t)$ 在常微系统中是不稳定解,则在偏微系统中也是不稳定的. $\phi(t)$ 在常微系统中稳定,则在偏微系统中也不一定稳定.

L^* 是 L 的共轭算子

$$L^*(s) \begin{pmatrix} u \\ v \end{pmatrix} = D \begin{pmatrix} \Delta u \\ \Delta v \end{pmatrix} + J^*(E_*) \begin{pmatrix} u \\ v \end{pmatrix}. \quad (4.6)$$

此处 $J_{E_*}^* = J_{E_*}^T, D_{L^*} = X_C$.

令

$$\theta = \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} = \begin{pmatrix} 1 \\ \frac{i\omega_2 - a_{11}}{a_{12}} \end{pmatrix}, \quad \theta^* = \begin{pmatrix} a_0^* \\ b_0^* \end{pmatrix} = \frac{1}{2\pi\omega_2} \begin{pmatrix} \omega_2 - a_{22}i \\ a_{12}i \end{pmatrix}.$$

显然,对任意的 $\gamma \in D_{L^*}$, $\beta \in D_L$ 有 $\langle L^*\gamma, \beta \rangle = \langle \beta, L\gamma \rangle$. 其中 $\langle \gamma, \beta \rangle = \int_0^\pi \bar{\gamma}^\tau \beta \, dr$ 并记作 $L^2[(0, \pi)] \times L^2[(0, \pi)]$ 的内积. $L\theta = i\omega_2\theta$, $L^*\theta^* = -i\omega_2\theta^*$, $\langle \theta^*, \theta \rangle = 1$, $\langle \theta^*, \bar{\theta} \rangle = 0$.

将 $X = X^C \oplus X^S$ 分解. $X^C := \{z\theta + \bar{z}\bar{\theta} : z \in C\}$, $X^S := \{w \in X : \langle \theta^*, w \rangle = 0\}$, 对任意的 $(u, v) \in X$, 存在 $z \in C$, $w = (w_1, w_2) \in X^S$ 使得:

$$(u, v)^\tau = z\theta + \bar{z}\bar{\theta} + (w_1, w_2)^\tau, \quad z = \langle \theta^*, (x, y)^\tau \rangle.$$

$$\begin{cases} u = z + \bar{z} + w_1 \\ v = z(\frac{i\omega_2 - a_{11}}{a_{12}}) + \bar{z}(\frac{-i\omega_2 + a_{22}}{a_{12}}) + w_2 \end{cases} \quad (4.7)$$

在 $\langle z, w \rangle$ 坐标系中

$$\begin{cases} \frac{dz}{dt} = i\omega_2 z + \langle \theta^*, \tilde{g} \rangle \\ \frac{dw}{dt} = Lw + H(z, \bar{z}, w) \end{cases} \quad (4.8)$$

其中 $\tilde{g} = (g_1, g_2)^\tau$, $H(z, \bar{z}, w) = \tilde{g} - \langle \theta^*, \tilde{g} \rangle \theta - \langle \bar{\theta}^*, \tilde{g} \rangle \bar{\theta}$. 根据以上定义不难得出:

$$\langle \theta^*, \tilde{g} \rangle = \frac{1}{2\omega_2} [\omega_2 g_1 + (a_{22}g_1 - a_{12}g_2)i]$$

$$\langle \bar{\theta}^*, \tilde{g} \rangle = \frac{1}{2\omega_2} [\omega_2 g_1 - (a_{22}g_1 - a_{12}g_2)i]$$

$$\langle \theta^*, \tilde{g} \rangle \theta = \frac{1}{2\omega_2} \begin{pmatrix} \omega_2 g_1 + (a_{22}g_1 - a_{12}g_2)i \\ [\omega_2 g_1 + (a_{22}g_1 - a_{12}g_2)i] \frac{i\omega_2 - a_{11}}{a_{12}} \end{pmatrix}$$

$$\langle \bar{\theta}^*, \tilde{g} \rangle \bar{\theta} = \frac{1}{2\omega_2} \begin{pmatrix} \omega_2 g_1 - (a_{22}g_1 - a_{12}g_2)i \\ [\omega_2 g_1 - (a_{22}g_1 - a_{12}g_2)i] \frac{-i\omega_2 - a_{11}}{a_{12}} \end{pmatrix}$$

综上可得 $H(z, \bar{z}, w) = \tilde{g} - \langle \theta^*, \tilde{g} \rangle \theta - \langle \bar{\theta}^*, \tilde{g} \rangle \bar{\theta} = (0, 0)^\tau$

记

$$w = \frac{w_{20}}{2} z^2 + w_{11} z \bar{z} + \frac{w_{20}}{2} \bar{z}^2 + o(|z|^3).$$

根据中心对折可得 $(2i\omega_2 - L)w_{20} = 0$, $-Lw_{11} = 0$, 以及 $w_{02} = \bar{w}_{20}$. 这也说明 $w_{20} = w_{02} = w_{11} = 0$.

$$\frac{dz}{dt} = i\omega_2 z + \frac{1}{2}g_{20}z^2 + g_{11}z\bar{z} + \frac{1}{2}g_{02}\bar{z}^2 + \frac{1}{2}g_{21}z^2\bar{z} + o(|z|^4). \quad (4.9)$$

$$g_{20} = \langle \theta^*, (c_0, d_0)^\tau \rangle, \quad g_{11} = \langle \theta^*, (e_0, f_0)^\tau \rangle, \quad g_{21} = \langle \theta^*, (g_0, h_0)^\tau \rangle.$$

$$\begin{aligned}
c_0 &= f_{1uu}a_0^2 + 2f_{1uv}a_0b_0 + f_{1vv}b_0^2 = 2a_{13} + 2a_{14}b_0 + 2a_{15}b_0^2. \\
d_0 &= f_{2uu}a_0^2 + 2f_{2uv}a_0b_0 + f_{2vv}b_0^2 = 2a_{23} + 2a_{24}b_0 + 2a_{25}b_0^2. \\
e_0 &= f_{1uu}|a_0|^2 + f_{1uv}(a_0\bar{b}_0 + \bar{a}_0b_0) + f_{1vv}|b_0|^2 = 2a_{13} + a_{14}(b_0 + \bar{b}_0) + 2a_{15}|b_0|^2. \\
f_0 &= f_{2uu}|a_0|^2 + f_{2uv}(a_0\bar{b}_0 + \bar{a}_0b_0) + f_{2vv}|b_0|^2 = 2a_{23} + a_{24}(b_0 + \bar{b}_0) + 2a_{25}|b_0|^2. \\
g_0 &= f_{1uuu}|a_0|^2a_0 + f_{1uuv}(2|a_0|^2b_0 + a_0^2\bar{b}_0) + f_{1uvv}(2a_0|b_0|^2 + \bar{a}_0b_0^2) + f_{1vvv}|b_0|^2b_0. \\
&= 6a_{16} + 2a_{17}(2b_0 + \bar{b}_0) + 2a_{18}(2|b_0|^2 + b_0^2) + 6a_{19}|b_0|^2b_0. \\
h_0 &= f_{2uuu}|a_0|^2a_0 + f_{2uuv}(2|a_0|^2b_0 + a_0^2\bar{b}_0) + f_{2uvv}(2a_0|b_0|^2 + \bar{a}_0b_0^2) + f_{2vvv}|b_0|^2b_0. \\
&= 6a_{26} + 2a_{27}(2b_0 + \bar{b}_0) + 6a_{29}|b_0|^2b_0.
\end{aligned}$$

由此可以算出:

$$\begin{aligned}
g_{20} &= \{a_{13} - \frac{2a_{11}(a_{15}a_{22} - a_{12}a_{25})}{a_{12}^2}\} \\
&+ \frac{i}{\omega_2}\{a_{13}a_{22} - a_{12}a_{23} + \frac{a_{14}(\omega_2^2 - a_{11}a_{22})}{a_{12}} + \frac{(a_{11}^2 - \omega_2^2)(a_{15}a_{22} - a_{12}a_{25}) - 2a_{11}a_{15}\omega_2^2}{a_{12}^2}\}. \\
g_{11} &= \{a_{13} - \frac{a_{11}a_{14}}{a_{12}} + \frac{(a_{11}^2 + \omega_2^2)a_{15}}{a_{12}^2}\} \\
&+ \frac{i}{\omega_2}\{a_{13}a_{22} - a_{12}a_{23} + a_{11}a_{24} + \frac{a_{11}a_{14}a_{22}}{a_{12}} + \frac{(a_{11}^2 + \omega_2^2)(a_{15}a_{22} - a_{12}a_{25})}{a_{12}^2}\} \\
g_{21} &= \{3a_{16} + a_{27} - \frac{a_{17}(3a_{11} + a_{22})}{a_{12}} + \frac{a_{18}(3a_{11}^2 + \omega_2^2 + 2a_{11}a_{22})}{a_{12}^2} \\
&- \frac{3(a_{11}^2 + \omega_2^2)a_{19}(a_{11} + a_{22}) - a_{12}a_{29}}{a_{12}^3}\} \\
&+ \frac{i}{\omega_2}\{3(a_{16}a_{22} - a_{12}a_{26} + a_{11}a_{27}) + \frac{a_{17}(\omega_2^2 - 3a_{11}a_{22})}{a_{12}} + \frac{a_{18}(a_{22}(3a_{11}^2 + \omega_2^2) - 2a_{11}\omega_2^2)}{a_{12}^2} \\
&+ \frac{(a_{11}^2 + \omega_2^2)(3a_{19}\omega_2^2 - a_{11}(a_{19}a_{22} - a_{12}a_{29}))}{a_{12}^3}\}.
\end{aligned}$$

根据Hassard et al. [16] (1981)

$$\begin{aligned}
Re(c_1) &= Re\{\frac{i}{2\omega_2}(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{1}{2}g_{21}\} \\
&= -\frac{1}{2\omega_2}\{Re g_{20}Im g_{11} + Im g_{20}Re g_{11}\} + \frac{1}{2}Re g_{21}.
\end{aligned}$$

假设定理 3 成立, 则系统(4.1)在 $C_1 = 0$ 时发生 Hopf 分支.

- (i) 如果 $Re(c_1) < 0$, 那么 Hopf 分支的分支周期解是轨道渐近稳定的且分支方向是亚临界的.
- (ii) 如果 $Re(c_1) > 0$, 那么 Hopf 分支的分支周期解是不稳定的且分支方向是超临界的.

5. 结论

在本文的研究中当对捕食者捕获率或恐惧因子的值较大时, 食饵种群的出生率很低时, 两个种群

都将灭绝;当对捕食者捕获率或恐惧因子的值较大时,系统表现出不同类型的复杂动力学:当出生率较高时,系统表现出双稳定性,一个是无捕食者平衡点,另一个是共存平衡点.

选取由食饵到捕食者的转化率 c 为参数,当 c 增加到临界值 $c^{[HB]}$ 时,系统(1.5) 在正平衡点 E^* 附近产生 Hopf 分支. 由第三节的结论表明: 选取适当初始条件和参数值时, 系统(1.5)会产生极限环.

进一步, 考虑捕食者与食饵在空间的扩散效应,在反应扩散系统中内部平衡点 E_* 的局部一致渐近稳定性与 Turing 不稳定性得到验证.由中心对折理论,选取适当的参数值,得到具有时间周期模式的反应扩散系统的 Hopf 分支的存在性,方向性以及分支周期解的稳定性.系统(4.1)会产生极限环即模型有捕食者与食饵数量的周期性震荡产生, 两者的数量呈现周期性振荡而共存.

参考文献

- [1] Holling, C.S. (1959) The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *The Canadian Entomologist*, **91**, 293-320.
<https://doi.org/10.4039/ent91293-5>
- [2] Holling, C.S. (1959) Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist*, **91**, 385-398. <https://doi.org/10.4039/ent91385-7>
- [3] Holling, C.S. (1965) The Functional Response of Predators to Prey Density and Its Role in Mimicry and Population Regulation. *Memoirs of the Entomological Society of Canada*, **97**, 5-60. <https://doi.org/10.4039/entm9745fv>
- [4] Majumdar, P., Debnath, S., Mondal, B., Sarkar, S. and Ghosh, U. (2022) Complex Dynamics of a Prey-Predator Interaction Model with Holling Type-II Functional Response Incorporating the Effect of Fear on Prey and Non-Linear Predator Harvesting. *Rendiconti del Circolo Matematico di Palermo Series 2*, **72**, 1017-1048. <https://doi.org/10.1007/s12215-021-00701-y>
- [5] Dawes, J.H.P. and Souza, M.O. (2013) A Derivation of Holling's Type I, II and III Functional Responses in Predator-Prey Systems. *Journal of Theoretical Biology*, **327**, 11-22.
<https://doi.org/10.1016/j.jtbi.2013.02.017>
- [6] Arsie, A., Kottegoda, C. and Shan, C. (2022) A Predator-Prey System with Generalized Holling Type IV Functional Response and Allee Effects in Prey. *Journal of Differential Equations*, **309**, 704-740. <https://doi.org/10.1016/j.jde.2021.11.041>
- [7] Huang, J., Ruan, S. and Song, J. (2014) Bifurcations in a Predator-Prey System of Leslie Type with Generalized Holling Type III Functional Response. *Journal of Differential Equations*, **257**, 1721-1752. <https://doi.org/10.1016/j.jde.2014.04.024>
- [8] Zaw Myint, A. and Wang, M. (2020) Dynamics of Holling-Type II Prey-Predator System with a Protection Zone for Prey. *Applicable Analysis*, **101**, 1833-1847.
<https://doi.org/10.1080/00036811.2020.1789595>

-
- [9] Li, X., Hu, G. and Lu, S. (2020) Pattern Formation in a Diffusive Predator-Prey System with Cross-Diffusion Effects. *Nonlinear Dynamics*, **100**, 4045-4060. <https://doi.org/10.1007/s11071-020-05747-8>
- [10] Wang, X., Zanette, L. and Zou, X. (2016) Modelling the Fear Effect in Predator-Prey Interactions. *Journal of Mathematical Biology*, **73**, 1179-1204. <https://doi.org/10.1007/s00285-016-0989-1>
- [11] Barman, D., Roy, J., Alrabaiah, H., Panja, P., Mondal, S.P. and Alam, S. (2021) Impact of Predator Incited Fear and Prey Refuge in a Fractional Order Prey Predator Model. *Chaos, Solitons Fractals*, **142**, Article 110420. <https://doi.org/10.1016/j.chaos.2020.110420>
- [12] Sasmal, S.K. (2018) Population Dynamics with Multiple Allee Effects Induced by Fear Factors—A Mathematical Study on Prey-Predator Interactions. *Applied Mathematical Modelling*, **64**, 1-14. <https://doi.org/10.1016/j.apm.2018.07.021>
- [13] Clark, C.W. (1979) Mathematical Models in the Economics of Renewable Resources. *SIAM Review*, **21**, 81-99. <https://doi.org/10.1137/1021006>
- [14] Krishna, S. (1998) Conservation of an Ecosystem through Optimal Taxation. *Bulletin of Mathematical Biology*, **60**, 569-584. <https://doi.org/10.1006/bulm.1997.0023>
- [15] Perko, L. (1996) *Differential Equations and Dynamical Systems*. Springer, 7.
- [16] Hassard, B.D., Kazarinoff, N.D. and Wan, Y.H. (1981) *Theory and Applications of Hopf Bifurcation*. Cambridge University Press.