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Predator–prey model with prey harvesting, cross diffusion, intraspecific predator competition, and periodic parameters

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Abstract. We develop a predator–prey model with logistic prey growth, linear predation, proportional harvesting, and predator intraspecific competition. Starting from an autonomous ordinary differential equation (ODE) model, we extend it to reaction–diffusion systems to capture spacial movement of populations. Periodic and non-autonomous equations incorporate seasonal and anthropogenic effects. We formulate a non-autonomous differential model with periodic parameters. We analyze the equilibrium stability, and derive conditions for Turing instability. We use coincidence degree theory to show the existence of positive periodic solutions. Numerical simulations illustrate spatial pattern formation and the influence of parameters on population dynamics.

Keywords: prey harvesting, intraspecific competition, cross diffusion, Turing pattern, non-autonomous model, periodic solution.

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1 Introduction

A century after Alfred J. Lotka (1925) and Vito Volterra (1926) independently introduced their the foundational predator–prey equations, these models remain central to understanding species interaction and population dynamics. The Lotka–Volterra framework formulated

through ordinary differential equations (ODEs) continues to appear in both theory and applications; see the short communication by Fort [6] "Lotka–Volterra at 100: How predator–prey modeling became a universal framework".

Temporal models assume a well-mixed environment, yet ecosystems are spatially heterogeneous. reaction–diffusion models address this by representing both self-diffusion (driven by intraspecific movement) and cross-diffusion (driven by prey avoiding predator rich zones or predators actively seeking prey dense areas). Introduced by Kerner [11] in 1959 and later applied by Shigesada et al. [22] in 1979, cross-diffusion can generate stationary spatial patterns via Turing instability. A. M. Turing [30] showed that a system of reacting and diffusing chemicals could evolve from initial near-homogeneity into spatial patterns of chemical concentration. Cross diffusion driven patterns have been linked to real-world ecological phenomena including predator–prey patchiness and spatial segregation, see [7,8,12,13,24,28,29,32,34].

Seasonal fluctuation and human activities, including harvesting, create time dependent variations in ecological patters. Non-autonomous models with periodic coefficients therefore offer a more realistic framework. There have been recent studies in this direction, see [3–5,14,15,23,31,35].

Let us mention some of the recent works that motivated our research. Wang et al. [32], inspired by the work in [21], studied the existence and Turing instability for positive solutions of

$$\begin{aligned}
\frac{\partial u}{\partial t} - d_u \Delta u &= ru - du^2 - \frac{cuv}{1+\alpha\xi+u+kv}, \quad x \in \Omega,\ t > 0,\\
\frac{\partial v}{\partial t} - d_v \Delta v &= \frac{\beta(u+\xi-\rho kv)v}{1+\alpha\xi+u+kv} - mv, \quad x \in \Omega,\ t > 0,\\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega,\ t > 0,\\
u(x,0) = u_0(x) \geq 0, \quad u_0 \not\equiv 0, \quad v(x,0) &= v_0(x) \geq 0, \quad v_0 \not\equiv 0, \quad x \in \Omega.
\end{aligned}$$

Bhutia et al. [2] studied a cross-diffusion and nonlocal competition model with harvesting,

$$\begin{aligned}
\frac{\partial u}{\partial t} &= ru\left(1-\frac{u}{k}\right) - \frac{\alpha uv}{a+u} - q_1 Eu + d_1 \frac{\partial^2 u}{\partial x^2}, \quad x \in \Omega,\ t > 0,\\
\frac{\partial v}{\partial t} &= \frac{\beta uv}{a+u} - mv - \delta v \int_\Omega \eta(x,y)v(y,t)\,dy - q_2 Ev + d_2 \frac{\partial^2 v}{\partial x^2}, \quad x \in \Omega,\ t > 0.
\end{aligned}$$

Yu et al. [35] investigated periodic solution of a non-autonomous Gause-type predator–prey model with Allee effect,

$$\begin{aligned}
\frac{du}{dt} &= r(t)\left(1-\frac{u}{k}\right)\big(x(t)-m(t)\big)u(t) - \frac{s(t)u(t)^2}{u(t)^2+a(t)^2}\,y(t) - E_1(t),\\
\frac{dv}{dt} &= p(t)\frac{u(t)^2}{u(t)^2+a(t)^2}v(t) - b(t)v(t) - E_2(t).
\end{aligned}$$

Pati [20] studied a logistic Lotka–Volterra predator–prey model with delayed harvesting of the prey,

$$\begin{aligned}
\frac{du(t)}{dt} &= ru(t)\left(-\frac{u(t)}{K}\right) - au(t)v(t) - qEu(t-\tau),\\
\frac{dv(t)}{dt} &= eau(t)y(t) - \mu v(t),
\end{aligned}$$

Ojha et al. [19] studied predator–prey and the impacts of anti-predator behavior, in autonomous and non-autonomous settings. Wang and Zhang [33] investigated effects of diffusion on a degenerate predator–prey model with cross-diffusion. Sun and Ma [25] studied a competition-competition-predation system with cross diffusion.

In this work, we study a predator–prey model that incorporates logistic prey growth, linear predation, harvesting of prey, and intraspecific competition among predators. Then we extend the model to a reaction–diffusion system with self-diffusion, and then to a cross-diffusion model. We further formulate a non-autonomous ODE model by introducing periodic time dependence into the ecological parameters.

This article is organized as follows. In Section 2, we present the base, an autonomous ODE, its self-diffusive and cross-diffusive PDE extensions, and a non-autonomous ODE formulation. In Section 3, we analyze the stability of the autonomous, self-diffusion, and cross-diffusion models. Also we derive conditions for Turing instability. In section 4, we show the existence of solutions for a non-autonomous model using coincidence degree theory. In Section 5, numerical simulations illustrate the theoretical results, and highlight the role of cross-diffusion in generating spatial patterns.

2 Formulation of models

In this section, we formulate a base model and its extensions to self diffusion, cross diffusion and non-autonomous models.

2.1 Baseline model

We start with a predator–prey system that includes logistic prey growth, linear predation, harvesting of prey, and intraspecific competition among predators.

$$\begin{aligned} \frac{du}{dt} &= ru\left(1-\frac{u}{k}\right) - auv - hu, \quad t > 0, \\ \frac{dv}{dt} &= abuv - \mu v^2, \quad t > 0, \\ u(0) &= u_0 \geq 0, \quad v(0) = v_0 \geq 0, \end{aligned} \tag{2.1}$$

where $u(t)$ and $v(t)$ denote the population densities of prey and predator, respectively. The parameters are defined as follows:

- a – attack rate of predator on prey,
- b – biomass conversion efficiency by predator from prey caught,
- h – harvesting effort applied to prey, including a catchability factor,
- k – carrying capacity for the prey population,
- μ – strength of intraspecific competition in the predator population,
- r – intrinsic growth rate of prey,

The prey population dynamics is influenced by three primary processes. First is the logistic growth $ru\left(1-\frac{u}{k}\right)$ that captures the increase constrained by environmental carrying capacity k. Second is the predation loss auv, caused by predators. Third is the harvesting loss hu.

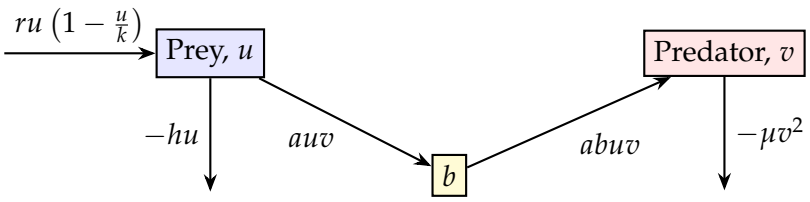

Figure 2.1: Schematic diagram of the predator–prey model

Harvesting plays a crucial role in shaping population dynamics. It can serve as a management tool to maintain ecological balance and ensure sustainable yields, but excessive or poorly regulated harvesting can lead to population decline, destabilization of predator–prey interactions, or even extinction. Incorporating harvesting terms allows us to study how it interacts with other ecological factors [9, 18]. In our model, harvesting is proportional, in contrast to the additive harvesting used in [35].

The predator population is governed by two mechanisms. First is the growth $abuv$ caused by consuming prey. Second is the Intraspecific competition μv^2. It refers to the interaction among individuals of the same species competing for limited resources. This competition becomes particularly significant when population density increases. In crowded conditions, individuals experience greater difficulty in accessing essential resources, leading to reduced reproduction rates or increased mortality [1, 10, 26, 27].

2.2 Self reaction–diffusion model

To incorporate spatial effects, we extend the ODE system (2.1) to a reaction–diffusion model that results in a system of partial differential equations,

$$\begin{aligned}
\frac{\partial u}{\partial t} &= d_{11}\Delta u + ru\left(1-\frac{u}{k}\right) - auv - hu, \quad x \in \Omega,\ t > 0,\\
\frac{\partial v}{\partial t} &= d_{22}\Delta v + abuv - \mu v^2, \quad x \in \Omega,\ t > 0,\\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega,\ t > 0,\\
u(x,0) = u_0(x) \geq 0,\ u_0 \not\equiv 0, &\quad v(x,0) = v_0(x) \geq 0,\ v_0 \not\equiv 0, \quad x \in \Omega,
\end{aligned} \tag{2.2}$$

where $u(x,t)$ and $v(x,t)$ represent the spatial densities of prey and predator, $d_{11} \geq 0$ and $d_{22} \geq 0$ are the self-diffusion coefficients, $\Omega \subset \mathbb{R}^n$, and $\Delta u = u_{x_1x_1} + u_{x_2x_2} + \cdots + u_{x_nx_n}$. The homogeneous Neumann boundary conditions imply that there is no flux across the boundary, modeling an isolated habitat.

2.3 Cross reaction–diffusion model

In real ecological systems, the movement of one species can be influenced by the density gradient of another species. This leads to the introduction of cross-diffusion terms. Our

model is partial differential equation

$$\begin{aligned}
\frac{\partial u}{\partial t} &= d_{11}\Delta u + d_{12}\Delta v + ru\left(1-\frac{u}{k}\right) - auv - hu, \quad x \in \Omega,\ t > 0,\\
\frac{\partial v}{\partial t} &= d_{21}\Delta u + d_{22}\Delta v + abuv - \mu v^2, \quad x \in \Omega,\ t > 0,\\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega,\ t > 0,\\
u(x,0) = u_0(x) \geq 0, &\quad u_0 \not\equiv 0, \quad v(x,0) = v_0(x) \geq 0, \quad v_0 \not\equiv 0, \quad x \in \Omega.
\end{aligned} \tag{2.3}$$

Here $d_{12}\Delta v$ and $d_{21}\Delta u$ indicate the influence of predator gradients on prey movement and the influence of prey gradients on predator movement, respectively. We assume the diffusion coefficients d_{11}, d_{12}, d_{21}, and d_{22} are non-negative. The cross-diffusion introduces a non-Fickian movement behavior and has been shown to be a critical mechanism in generating spatial heterogeneity through Turing instability.

2.4 Non-autonomous model

To incorporate environmental seasonality and human-induced fluctuations, we extend the base predator–prey model (2.1) by allowing certain parameters to vary periodically with time. The intrinsic growth rate $r(t)$, predator's attack rate $a(t)$, and harvesting effort $h(t)$ depend on seasonal fluctuations such as resources availability, temperature, reproductive cycles, and habitat structure. The harvesting effort $h(t)$ depends on open/closed harvesting seasons, regulatory cycles, or economic activity patterns. The harvesting may not agree with starting of the seasonal cycles, so include a phase shift ϕ. The resulting non-autonomous system is

$$\begin{aligned}
\frac{du}{dt} &= r(t)u\left(1-\frac{u}{k}\right) - a(t)uv - h(t)u,\\
\frac{dy}{dt} &= a(t)buv - \mu v^2,
\end{aligned} \tag{2.4}$$

where the time-dependent parameters are assumed to be continuous and T-periodic. For example

$$\begin{aligned}
a(t) &= \bar{a}\big(1 + \alpha_a \cos(\omega t)\big),\\
h(t) &= \bar{h}\big(1 + \alpha_h \sin(\omega t + \phi)\big),\\
r(t) &= \bar{r}\big(1 + \alpha_r \sin(\omega t)\big),
\end{aligned}$$

with $\bar{a}$, $\bar{h}$, $\bar{r}$, representing the average values of predator attack rate, harvesting effort, and prey growth rate, respectively. The parameters α_a, α_h, and α_r, and $(0 \leq \alpha_i \leq 1)$ determine their amplitudes, while $\omega = 2\pi/T$ is the frequency, and ϕ is a phase shift.

3 Stability of equilibrium solutions

3.1 Stability for the base model

Model (2.1) has three equilibrium solutions. The first solution is $u = 0$ and $v = 0$. This can be caused by the initial conditions or by the prey dying out and therefore the predator dying out later.

The second solution is semi-trivial with $v = 0$, which can be caused by the initial condition on predators or by $ab = 0$. If the predator goes extinct, we set $\mu = 0$ to avoid v having negative values. When $v = 0$, system (2.1) becomes the logistic model with harvesting,

$$\frac{du}{dt} = ru\left(1 - \frac{u}{k}\right) - hu.$$

The solution to this equation yields the equilibrium solution to (2.1), with $u = k\left(1 - \frac{h}{r}\right)$ and $v = 0$.

The third equilibrium solution is obtained by setting the right-hand sides of (2.1) to zero. This yields

$$u^* = \frac{k\mu(r-h)}{\mu r + a^2bk}, \qquad v^* = \frac{ab}{\mu}u^*. \tag{3.1}$$

Note that the denominator is not zero, because we assumed $ab > 0$. Also note u^* and v^* are positive constants.

To avoid depleting the prey, we assume that the grow rate is larger than the harvesting rate, i.e.

$$r > h \tag{3.2}$$

To analyze the stability of equilibrium solutions, we need to compute the eigenvalues of the Jacobian matrix

$$J(u,v) = \begin{pmatrix} D_1(u,v) & D_2(u,v) \\ D_3(u,v) & D_4(u,v) \end{pmatrix} \tag{3.3}$$

where

$$D_1(u,v) = r\left(1 - \frac{2u}{k}\right) - av - h, \qquad D_2(u,v) = -au,$$
$$D_3(u,v) = abv, \qquad D_4(u,v) = abu - 2\mu v.$$

The eigenvalues are the roots of the characteristic equation

$$\lambda^2 - \operatorname{tr}\big(J(u,v)\big)\lambda + \det\big(J(u,v)\big) = 0,$$

where $\operatorname{tr}(J) = D_1 + D_4$ and $\det(J) = D_1D_4 - D_2D_3$.

First we analyze the equilibrium point $(0,0)$ of (2.1). The eigenvalues are $\lambda_1 = 0$ and $\lambda_2 = r - h$. By assumption (3.2), λ_2 is positive so that this equilibrium point is unstable.

For the semi-trivial solution, $u = k(1 - \frac{h}{r})$ and $v = 0$, the eigenvalues are $\lambda_1 = -(r-h) < 0$ and $\lambda_2 = \frac{abk}{r}(r-h) > 0$. This yields a saddle point, and makes this equilibrium point unstable.

For the equilibrium (u^*, v^*) given by (3.1), the Jacobian has

$$\operatorname{tr}\big(J(u^*,v^*)\big) = -\frac{\mu(r-h)(r+abk)}{\mu r + a^2bk} < 0, \qquad \det\big(J(u^*,v^*)\big) = \frac{abk\mu(r-h)^2}{\mu r + a^2bk} > 0.$$

Because $\operatorname{tr}(J)$ is negative and $\det(J)$ is positive the characteristic equation has two roots (the eigenvalues) whose real parts are negative. Therefore, the equilibrium point is asymptotically stable which is stated in the following theorem.

Theorem 3.1. *Under assumption (3.2), the equilibrium solution (u^*, v^*) of (2.1) is a locally asymptotically stable.*

3.2 Stability for the self reaction–diffusion model

Since the solution (u^*, v^*) of (2.1) is constant with respect to x, we have $\Delta u^* = \Delta v^* = 0$ which makes (u^*, v^*) a solution to (2.2). We consider (2.2) as a perturbation of (2.1), and define $u = u^* + \tilde{u}$ and $v = v^* + \tilde{v}$. Then the linearization of (2.2) leads to the system

$$\begin{aligned} \frac{\partial \tilde{u}}{\partial t} &= d_{11}\Delta\tilde{u} + \left[r\left(1 - \frac{2u^*}{k}\right) - av^* - h\right]\tilde{u} - au^*\tilde{v} \\ \frac{\partial \tilde{v}}{\partial t} &= d_{22}\Delta\tilde{v} + abv^*\tilde{u} + (abu^* - 2\mu v^*)\tilde{v}\,. \end{aligned} \tag{3.4}$$

Let σ be the eigenvalue, and α be a wave number of system (2.1). Then the change of variables

$$\tilde{u} = \bar{u}e^{\sigma t}\sin(\alpha x) \quad \text{and} \quad \tilde{v} = \bar{v}e^{\sigma t}\sin(\alpha x),$$

with $\bar{u}$ and $\bar{u}$ constant, transforms system (2.1) into

$$\sigma\begin{pmatrix}\bar{u}\\ \bar{v}\end{pmatrix} = J_d((u^*, v^*)\begin{pmatrix}\bar{u}\\ \bar{v},\end{pmatrix}$$

where the Jacobian matrix is

$$J_d = \begin{pmatrix} D_1(u^*, v^*) - \alpha^2 d_{11} & D_2(u^*, v^*) \\ D_3(u^*, v^*) & D_4(u^*, v^*) - \alpha^2 d_{22}\,. \end{pmatrix}$$

Then the characteristic equation for $J_d(u^*, v^*)$ is

$$\sigma^2 - \operatorname{tr}(J_d(u^*, v^*))\sigma + \det(J_d(u^*, v^*)) = 0,$$

with

$$\begin{aligned} \operatorname{tr}(J_d(u^*, v^*)) &= -\big(d_{11} + d_{22}\big)\alpha^2 + \operatorname{tr}(J(u^*, v^*)\big), \\ \det(J_d(u^*, v^*)) &= d_{11}d_{22}\alpha^4 - \Big(d_{11}D_4(u^*, v^*) + d_{22}D_1(u^*, v^*)\Big)\alpha^2 + \det\big(J(u^*, v^*)\big). \end{aligned}$$

Since $d_{11} \geq 0$, $d_{22} \geq 0$, and $\operatorname{tr}\big(J(u^*, v^*)\big) < 0$, it follows that $\operatorname{tr}(J_d(u^*, v^*)) < 0$. Regarding the determinant, we have

$$\begin{aligned} \Big(d_{11}D_4(u^*, v^*) + d_{22}D_1(u^*, v^*)\Big) &= -d_{11}abu^* + d_{22}\left[(r - h) - \left(\frac{2r}{k} + \frac{a^2 b}{\mu}\right)u^*\right] \\ &= -d_{11}abu^* - d_{22}(r - h)\frac{\mu r}{\mu r + a^2 bk} < 0. \end{aligned}$$

So the coefficient of α^2 becomes positive, which makes $\det(J_d(u^*, v^*))$ positive. Then the solution σ to the quadratic equation has both roots with negative real part and this equilibrium point is asymptotically stable. This is stated as a theorem.

Theorem 3.2. *Let* (3.2) *hold. Then the equilibrium solution* (u^*, v^*) *of* (2.2) *is asymptotically stable.*

Note that stability of solutions to (2.1), (2.2), and (2.3) does not depend on the initial conditions, as long as the initial conditions are positive.

3.3 Turing instability for the cross reaction–diffusion model

In this section, we assume that the diffusion matrix

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}$$

is positive definite, equivalently

$$d_{11} > 0, \quad d_{22} > 0, \quad \text{and} \quad d_{11}d_{22} - d_{21}d_{12} > 0\,. \tag{3.5}$$

As in the previous section, we regard (2.3) as a perturbation of (2.1). Then the Jacobian matrix is

$$J_{cd}(u^*, v^*) = \begin{pmatrix} D_1(u^*, v^*) - \alpha^2 d_{11} & D_2(u^*, v^*) - \alpha^2 d_{12} \\ D_3(u^*, v^*) - \alpha^2 d_{21} & D_4(u^*, v^*) - \alpha^2 d_{22} \end{pmatrix}. \tag{3.6}$$

Then the characteristic equation for $J_{cd}(u^*, v^*)$ is

$$\sigma^2 - \mathrm{tr}(J_{cd}(u^*, v^*))\sigma + \det(J_{cd}(u^*, v^*)) = 0, \tag{3.7}$$

where $\mathrm{tr}\left(J_{cd}(u^*, v^*)\right) = \mathrm{tr}\left(J_d(u^*, v^*)\right) < 0$, and

$$\begin{aligned} \det\left(J_{cd}(u^*, v^*)\right) &= (d_{11}d_{22} - d_{12}d_{21})\alpha^4 \\ &\quad - \Big(d_{11}D_4(u^*, v^*) + d_{22}D_1(u^*, v^*) - d_{21}D_2(u^*, v^*) - d_{12}D_3(u^*, v^*)\Big)\alpha^2 \\ &\quad + \Big(D_1(u^*, v^*)D_4(u^*, v^*) - D_2(u^*, v^*)D_3(u^*, v^*)\Big). \end{aligned} \tag{3.8}$$

The first term of the above expression is $\det(D) > 0$ and the third term is $\det\left(J(u^*, v^*)\right) > 0$. If the second term of (3.8) is non-negative, i.e.

$$d_{11}D_4 + d_{22}D_1 - d_{12}D_2 - d_{12}D3 \geq 0, \tag{3.9}$$

then $\det\left(J_{cd}(u^*, v^*)\right) > 0$ and (u^*, v^*) is an asymptotically stable solution of for system (2.3).

On the other hand, if the second term of (3.8) is negative and large enough, $\det(J_{cd}(u^*, v^*)) < 0$ which leads to Turing instability. So we look for conditions that imply $\det(J_{cd}(u^*, v^*)) < 0$.

Note that (3.8) is a quadratic polynomial of α^2, whose graph is a parabola that opens up; so minimum happens at the vertex

$$\alpha^2 = \frac{d_{11}D_4 + d_{22}D_1 - d_{21}D_2 - d_{12}D_3}{2(d_{11}d_{22} - d_{12}d_{21})}$$

and

$$\det\left(J_{cd}(u^*, v^*)\right) = D_1D_4 - D_2D_3 - \frac{\left(d_{11}D_4 + d_{22}D_1 - d_{21}D_2 - d_{12}D_3\right)^2}{4(d_{11}d_{22} - d_{12}d_{21})}\,.$$

Here we omitted the variables (u^*, v^*) in D_1 D_2, D_3, and D_4, which are given by (3.1) and (3.3).

Therefore, a sufficient condition for $\det\left(J_{cd}(u^*, v^*)\right) < 0$, and hence for Turing instability, is

$$D_1D_4 - D_2D_3 < \frac{\left(d_{11}D_4 + d_{22}D_1 - d_{21}D_2 - d_{12}D_3\right)^2}{4(d_{11}d_{22} - d_{12}d_{21})}\,. \tag{3.10}$$

This inequality can be written as

$$4\det(J)\det(D) < \left(\det\begin{pmatrix} d_{11} & d_{12} \\ D_3 & D_4 \end{pmatrix} + \det\begin{pmatrix} D_1 & D_2 \\ d_{21} & d_{22} \end{pmatrix}\right)^2.$$

Under assumption (3.10), the equation $\det\left(J_{cd}(u^*, v^*)\right) = 0$ has two positive roots:

$$\alpha_{1,2}^2 = \frac{\left(d_{11}D_4 + d_{22}D_1 - d_{21}D_2 - d_{12}D_3\right) \pm \sqrt{\Delta}}{4(d_{11}d_{22} - d_{12}d_{21})},$$

where

$$\Delta = \left(d_{11}D_4 + d_{22}D_1 - d_{21}D_1 - d_{12}D_3\right)^2 - 4(d_{11}d_{22} - d_{12}d_{21})\left(D_1D_4 - D_2D_3\right).$$

For α^2 between these to roots, we have Turing instability, as stated in the next theorem.

Theorem 3.3. *Suppose that* (3.2) *and* (3.5) *hold. If* (3.10) *is satisfied, then the equilibrium point* (u^*, v^*) *for system* (2.3) *is unstable. Moreover, these conditions give rise to a Turing pattern for values of* α^2 *in the interval* (α_1^2, α_2^2).

On the other hand, if (3.9) *is satisfied, then solution* (u^*, v^*) *is asymptotically stable.*

4 Existence of solutions to the non-autonomous system

We have 3 equilibrium solutions. If the prey goes extinct, then the predator also goes extinct. This leads to the trivial solution $(0, 0)$. If the predator goes extinct, (2.4) becomes a logistic equation with harvesting,

$$\frac{du}{dt} = r(t)u(t)\left(1 - \frac{u(t)}{k}\right) - h(t)u(t)$$

which has the constant solutions $u = 0$ and

$$u = k\left(1 - \frac{h(t)}{r(t)}\right).$$

To avoid predators going extinct, we assume that $a(t)b > 0$ so predators always have food that is converted into biomass. By setting the right-hand sides of (2.4) to zero we find a solution whose components are positive, prey

$$u^* = \frac{k\mu\left(r(t) - h(t)\right)}{\mu r(t) + (a(t))^2 bk}$$

and predator

$$v^* = \frac{a(t)b}{\mu}u^* = \frac{a(t)bk\left(r(t) - h(t)\right)}{\mu r(t) + (a(t))^2 bk}.$$

Provided these two components of the solution are constant. The next task is to obtain solutions that are not constant, for example T-periodic solutions, assuming the coefficients are T-periodic. To do this we use coincidence degree theory, with the following notation.

Let Z and W be real Banach spaces, and let $L : \mathrm{dom}(L) \subset Z \to W$ be a Fredholm operator of index zero. If $P : Z \to Z$ and $Q : W \to W$ are continuous projectors such that $\mathrm{im}(P) = \ker(L)$, $\ker(Q) = \mathrm{im}(L)$, $Z = \ker(L) \oplus \ker(P)$, and $W = \mathrm{im}(L) \oplus \mathrm{im}(Q)$, then $L|_{\mathrm{dom}(L)\cap\ker(P)}$:

$\operatorname{dom}(L) \cap \ker(P) \to \operatorname{im}(L)$ has a generalized inverse operator denoted by K_p. If Ω is an open bounded subset of Z such that $\operatorname{dom}(L) \cap \Omega \neq 0$, then a mapping $N : Z \to W$ will be called L-compact on $\bar{\Omega}$, provided that $QN(\bar{\Omega})$ is bounded and $K_p(I - Q)N : \bar{\Omega} \to Z$ is compact.

For the abstract equation $Lz = Nz$ to be solvable we have the following theorem from [17, Theorem 2.4, p. 84].

Theorem 4.1. *Let L be a Fredholm operator of index zero and let N be an L-compact on $\bar{\Omega}$. Assume the following conditions are satisfied*

(1) $Lz \neq \lambda Nz$ for every $(z, \lambda) \in [(\operatorname{dom}(L) \setminus \ker(L)) \cap \partial\Omega] \times (0, 1)$;

(2) $Nz \notin \operatorname{im}(L)$ for every $z \in \ker(L) \cap \partial\Omega$;

(3) $D_0(QN|_{\ker(L)}, \ker(L) \cap \Omega) \neq 0$, where $Q : W \to W$ is a projector as above with $\operatorname{im}(L) = \ker(Q)$.

Then the equation $Lz = Nz$ has at least one solution in $\operatorname{dom}(L) \cap \bar{\Omega}$.

Since we are interested in solutions (u, v) with positive components, we can use the change of variables

$$u(t) = e^{z_1(t)}, \quad v(t) = e^{z_2(t)}.$$

So that (2.4) becomes

$$\begin{aligned} \frac{dz_1}{dt} &= r(t)\left(1 - \frac{e^{z_1(t)}}{k}\right) - a(t)e^{z_2(t)} - h(t), \quad t > 0, \\ \frac{dz_2}{dt} &= a(t)be^{z_1(t)} - \mu e^{z_2(t)}, \quad t > 0. \end{aligned} \tag{4.1}$$

Now we look for solutions (z_1, z_2) with components that can be positive, negative, or zero. We set up the coincidence degree theorem as follows. Let $Z = W$ be the Banach space consisting of pairs on functions (z_1, z_2) with components in $C(\mathbb{R}, \mathbb{R})$ and such that $z_i(t + T) = z_i(t)$ for all $t \in \mathbb{R}$ and $i = 1, 2$. In Z and W, we use the norm

$$\|z\| = \max_{0 \le t \le T} |z_1(t)| + \max_{0 \le t \le T} |z_2(t)|.$$

We define the operator L with domain $\operatorname{dom}(L)$ consisting of pairs of functions that have continuous fist derivative and are T-periodic.

$$L : \operatorname{dom}(L) \to W, \qquad L(z_1, z_2) = \left(\frac{dz_1}{dt}, \frac{dz_2}{dt}\right).$$

The kernel of L consists of pairs of constant functions; i.e. $\ker(L) = \mathbb{R}^2$, whose dimension is 2. Since the derivative of a T-periodic function is also T-periodic, the range of L consists of pairs of continuous T-periodic functions; thus

$$\operatorname{im}(L) = \left\{(z_1, z_2) \in W : \frac{1}{T}\int_0^T z_i(s)\, ds = 0,\ i = 1, 2\right\}.$$

Now we define the projections operators $P : Z \to Z$ and $Q : W \to W$ by

$$P(z_1, z_2) = Q(z_1, z_2) = \left(\frac{1}{T}\int_0^T z_1(s)\, ds,\ \frac{1}{T}\int_0^T z_2(s)\, ds\right).$$

Note that P has range consisting of pairs of constants, which is precisely the kernel of L, i.e. $\operatorname{im}(P) = \ker(L)$. Since each periodic function can be written as its average plus a function with zero average, we can write $Z = \ker(L) \oplus \ker(P)$. Also note that the kernel of Q consists of pairs of T-periodic functions whose average is zero, this is precisely the range of L, i.e. $\operatorname{im}(L) = \ker(Q)$. Using again that each periodic function can be written as its average plus a function with zero average, we can write $W = \operatorname{im}(Q) \oplus \operatorname{im}(L)$.

The only pair of constants that is in the range of L is $(0,0)$ thus the cokernel of L has dimension 2. In summary L is closed, unbounded, densely define on Z, and $\dim\ker(L) = \dim\operatorname{coker}(L) = 2$. Therefore, L is a Fredholm operator of index zero.

We define the operator $N : Z \times W \to W$ by

$$N(z(t),t) = \big(\Gamma_1(z,t), \Gamma_2(z,t)\big),$$

where Γ_1 and Γ_2 are the right-hand sides of (2.4); i.e.

$$\begin{aligned}
\Gamma_1(z(t),t) &= r(t)\left(1 - \frac{e^{z_1(t)}}{k}\right) - a(t)e^{z_2(t)} - h(t),\\
\Gamma_2(z(t),t) &= a(t)be^{z_1(t)} - \mu e^{z_2(t)},
\end{aligned}$$

where $z = (z_1, z_2)$. Since a, h, z_1, z_2 are continuous and T-periodic, so are Γ_1 and Γ_2. In particular if $z = (z_1, z_2)$ belongs to a bounded set $\Omega \subset Z$, say $|z_1| \le M$ and $|z_2| \le M$, then

$$\begin{aligned}
|\Gamma_1(z(t),t)| &\le \max_{0\le t\le T}\{r(t)\} + \max_{0\le t\le T}\{a(t)\}e^M + \max_{0\le t\le T}\{h(t)\},\\
|\Gamma_2(z(t),t)| &\le \max_{0\le t\le T}\{a(t)\}be^M + \mu e^M,
\end{aligned}$$

for all $t \in [0,T]$. Adding these two inequalities we obtain an upper bound $\tilde{M}$, such that $\|N(\Omega \times [0,t])\| \le \tilde{M}$. Then the projection $QN(\Omega \times [0,t])$ has also the same bound.

To show that N is L-compact, we use the Arzelà–Ascoli theorem. First we define the generalized inverse of L as $K_p :\in L \to \ker(P) \cap \operatorname{dom}(L)$ by

$$K_p(w) = \int_0^t w(s)\,ds - \frac{1}{T}\int_0^T \int_0^t w(s)\,ds\,dt\,.$$

It is easy to check that $L(K_p(w(t)) = \frac{d}{dt}(K_p(w(t)) = w(t)$.

Now we show that for each bounded subset $\Omega \subset Z$, the set $K_p(I-Q)N(\Omega \times [0,T])$ is bounded. For each $z \in \Omega$, we have

$$\begin{aligned}
\|K_p(I-Q)N(z,t)\| &= \left\| \int_0^t (I-Q)N(z,s)\,ds - \frac{1}{T}\int_0^t (I-Q)N(z,s)\,ds \right\|\\
&\le \int_0^t \|N(z,s)\|\,ds + \frac{1}{T}\int_0^t \|N(z,s)\|\,ds\\
&\le \frac{3T}{2}\tilde{M}\,.
\end{aligned}$$

To show that functions in $K_p(I-Q)N(\Omega \times [0,T])$ are equi-continuous, we find a common bound for their derivatives. For each $z \in \Omega$, from the definition of the generalized inverse, we have

$$\left\| \frac{d}{dt}\big[K_p(I-Q)N(z,t)\big] \right\| = \big\|(I-Q)N(z,t)\big\| \le \tilde{M}\,.$$

Therefore, $K_p(I-Q)N(\Omega\times[0,T])$ is compact and N is L-compact.

For the next theorem, we need the following constants:

$$M_1 := k\max_{0\le t\le T}\left\{1-\frac{h(t)}{r(t)}\right\}, \qquad M_2 := \max_{0\le t\le T}\{a(t)\}\frac{bM_1}{\mu},$$
$$M_3 := k\min_{0\le t\le T}\left\{1-\frac{a(t)M_2+h(t)}{r(t)}\right\}, \qquad M_4 := \min_{0\le t\le T}\{a(t)\}\frac{bM_3}{\mu}.$$

Note that if M_1 is positive, so is M_2. Also if M_3 is positive so is M_4.

Theorem 4.2. *Assume $0 < M_1$ and $0 < M_3$. Also assume that $a(t)$, $r(t)$, $h(t)$ are continuous, positive, and T-periodic functions with $r(t) > h(t)$. Then system (2.4) has at least one T-periodic solution with positive components.*

Proof. We have already done the setting for the coincidence degree theory. For (1) of Theorem 4.1, equation (4.1) is rewritten as $L(z(t) = N(z,t)$. For (1) in Theorem 4.1 we have

$$\begin{aligned}\frac{dz_1}{dt} &= \lambda\left[r(t)\left(1-\frac{e^{z_1(t)}}{k}\right)-a(t)e^{z_2(t)}-h(t)\right],\\ \frac{dz_2}{dt} &= \lambda\left[a(t)be^{z_1(t)}-\mu e^{z_2(t)}\right],\end{aligned} \tag{4.2}$$

for all $t\in[0,T]$. The strategy is to define a constant M such that the interior of the ball

$$\Omega = \{z\in Z : |z| < M\}$$

contains all solutions of (4.2) for all $\lambda\in(0,1)$. This way there are no solutions on the boundary of this ball, and part (1) of Theorem 4.1 is satisfied.

Let $\lambda\in(0,1)$ be fixed and $z=(z_1,z_2)$ be a solution of (4.2). Since z_1 and z_2 are continuous on $[0,T]$, they attain their maximum and minimum: $\max\{z_1(t)\} = z_1(t_1)$, $\max\{z_2(t)\} = z_2(t_2)$, $\min\{z_1(t)\} = z_1(t_3)$, and $\min\{z_2(t)\} = z_2(t_4)$. Then $z_1'(t_1) = z_1'(t_2) = z_2'(t_3) = z_2'(t_4) = 0$. From the first equation (4.2), we have

$$0 = \lambda\left[r(t_1)\left(1-\frac{e^{z_1(t_1)}}{k}\right)-a(t_1)e^{z_2(t_1)}-h(t_1)\right] < \lambda\left[r(t_1)\left(1-\frac{e^{z_1(t_1)}}{k}\right)-h(t_1)\right].$$

Then solving for $e^{z_1(t_1)}$ we have

$$e^{z_1(t)} \le e^{z_1(t_1)} < k\left(1-\frac{h(t_1)}{r(t_1)}\right) \le M_1, \qquad \forall t\in[0,T].$$

From the second equation (4.2), we have

$$0 = \lambda\left[a(t_2)be^{z_1(t_2)}-\mu e^{z_2(t_2)}\right].$$

Solving for $e^{z_2(t_2)}$, and using the inequality for $M_!$, we have

$$e^{z_2(t)} \le e^{z_2(t_2)} < a(t_2)\frac{bM_1}{\mu} \le M_2, \qquad \forall t\in[0,T].$$

Using this inequality in the first equation (4.2), we have

$$0 = \lambda\left[r(t_3)\left(1-\frac{e^{z_1(t_3)}}{k}\right)-a(t_3)e^{z_2(t_3)}-h(t_3)\right] > \lambda\left[r(t_3)\left(1-\frac{e^{z_1(t_3)}}{k}\right)-a(t_3)M_2-h(t_3)\right]$$

solving for $e^{z_1(t_3)}$, we have

$$e^{z_1(t)} \geq e^{z_1(t_3)} > k\left(1 - \frac{a(t_3)M_2 + h(t_3)}{r(t_3)}\right) \geq M_3, \quad \forall t \in [0,T]\,.$$

Using this inequality in the second equation (4.2), we have

$$0 = \lambda\left[a(t_4)be^{z_1(t_4)} - \mu e^{z_2(t_4)}\right] > \lambda\left[a(t_4)bM_3 - \mu e^{z_2(t_4)}\right].$$

Solving for $e^{z_2(t_4)}$, we have

$$e^{z_2(t)} \geq e^{z_2(t_4)} > a(t_4)\frac{bM_3}{\mu} \geq M_4, \qquad \forall t \in [0,T]\,.$$

At this moment we can define Ω that satisfies condition (1), but we want to satisfy (2) of theorem 4.1 at the same time.

For satisfying (2), we show that any function z in $\ker(L)$ satisfying $N(z) \in \operatorname{im}(L)$ is in the interior of Ω, hence not on the boundary. Let $z^* = (z_1^*, z_2^*)$ be in $\ker(L)$. Then z_1^* and z_2^* are constant functions. Computing $N(z^*)$ yields the right-hand side of (4.1). For this pair of functions to be in the range of L we need

$$\frac{1}{T}\int_0^T r(t)\left(1 - \frac{e^{z_1*}}{k}\right) - a(t)e^{z_2*} - h(t)\,dt = 0,$$
$$\frac{1}{T}\int_0^T a(t)be^{z_1^*} - \mu e^{z_2^*}\,dt = 0\,.$$

Equivalently,

$$\bar{r}\left(1 - \frac{e^{z_1*}}{k}\right) - \bar{a}e^{z_2*} - \bar{h} = 0,$$
$$\bar{a}be^{z_1^*} - \mu e^{z_2^*} = 0\,.$$

This system has solution

$$e^{z_1^*} = \frac{k\mu(\bar{r} - \bar{h})}{\mu\bar{r} + \bar{a}^2bk}, \qquad e^{z_2^*} = \frac{\bar{a}b}{\mu}e^{z_1^*}\,, \tag{4.3}$$

where the bar on top means the average, $\bar{r} = \frac{1}{T}\int_0^T r(s)\,ds$.

Let

$$\Omega = \{z \in Z : \|z\| < 1 + \max\{|z_1^*| + |z_2^*|, \max\{|\ln(M_1)|, |\ln(M_3)|\} + \max\{|\ln(M_2)|, |\ln(M_4)|\}\}.$$

Certainly, if for a $\lambda \in (0,1)$, (4.2) has a solution, then it is in the interior of Ω, so that (4.2) does not have solution on the boundary of Ω. On the other hand if (4.2) does not have solution, (4.2) does not have solution on the boundary of Ω. This proves condition (1) of Theorem 4.1.

For condition (2), we see that the only element z^* that is in $\ker(L)$ and $N(z^*) \in \operatorname{im}(L)$ is in the interior of Ω and cannot be on the boundary.

To prove condition (3) of Theorem 4.1, we find a solution of $QN(z_1, z_2) = 0$ that is in $\Omega \cap \ker(L)$. This solution is given by (4.3), and the Jacobian is

$$J_{QN}(z_1^*, z_2^*) = \begin{pmatrix} -\frac{\bar{r}}{k}e^{z_1^*} & -\bar{a}e^{z_1^*} \\ \bar{a}be^{z_1^*} & -\mu e^{z_2^*} \end{pmatrix}.$$

Then

$$\det\left(J_{QN}(z_1^*, z_2^*)\right) = \left(\frac{\bar{r}\mu}{k} + \bar{a}^2 b\right) e^{z_1^* + z_2^*} \neq 0\,.$$

and

$$\begin{aligned} D_0(QN|_{\ker(L)}, \ker(L) \cap \Omega) &= \deg(QN(z_1, z_2), \Omega \cap \ker(L), (0,0)) \\ &= |\operatorname{sign} \det\left(J_{QN}(z_1^*, z_2^*)\right)| = 1 \neq 0\,. \end{aligned}$$

We have verified all the requirements of the coincidence degree theorem 4.1. So system (2.4) has at least one T-periodic solution with positive components. □

5 Examples and numerical simulations

In this section, we gain more comprehensive dynamics of the autonomous and non-autonomous systems by utilizing numerical simulations, simultaneously confirming the validity of our theoretical results.

5.1 ODE model with self diffusion and cross diffusion

Example 5.1. Consider (2.1) with $r = 1$, $k = 1$, $a = 2$, $h = 0.125$, $b = 0.8$, and $\mu = 2.0$. With these values, (3.2) is satisfied. The equilibrium solution with positive components is $u^* = 0.3365$, $v^* = 0.2692$ which is stable, while $u = 0$, $v = 0$ is unstable. See Figure 5.1.

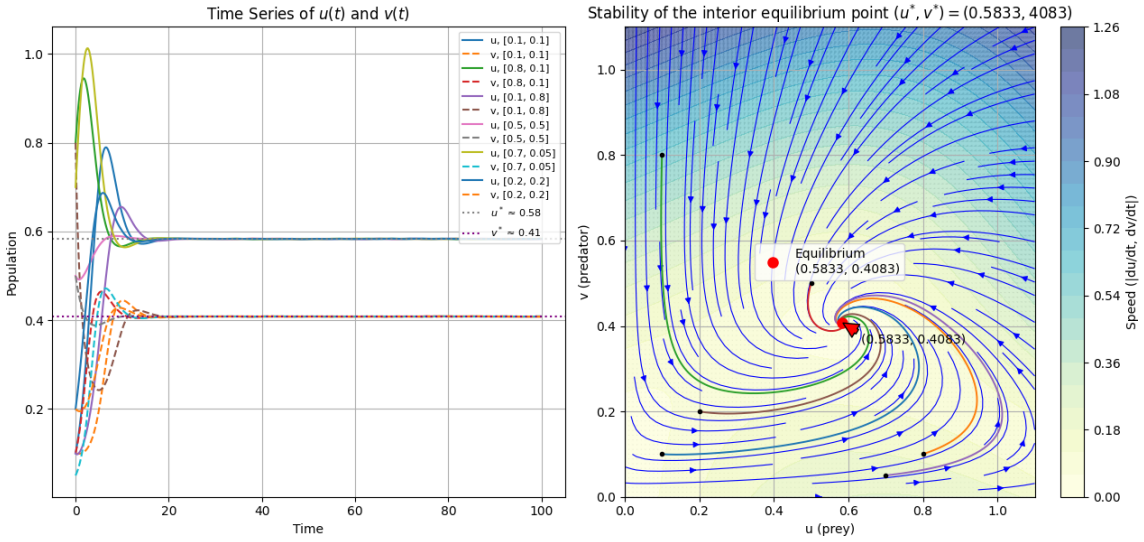

Figure 5.1: Time series and phase portrait of (u, v). Any solution starting near $(0, 0)$ are moving away from $(0, 0)$ and converging to the point $(0.3365, 0.2692)$.

Next, we consider the self reaction–diffusion problem (2.2). By Theorem 3.2, the equilibrium point $(0.3365, 0.2692)$ is stable for any $d_{11} > 0$ and $d_{22} > 0$. Using numerical simulations, Figure 5.2 confirms the absence of spatial pattern formation.

Next, we investigate the cross reaction–diffusion model, by including values for d_{12}, and d_{21} in the previous example. See Figures 5.3, 5.4, 5.5, and 5.6.

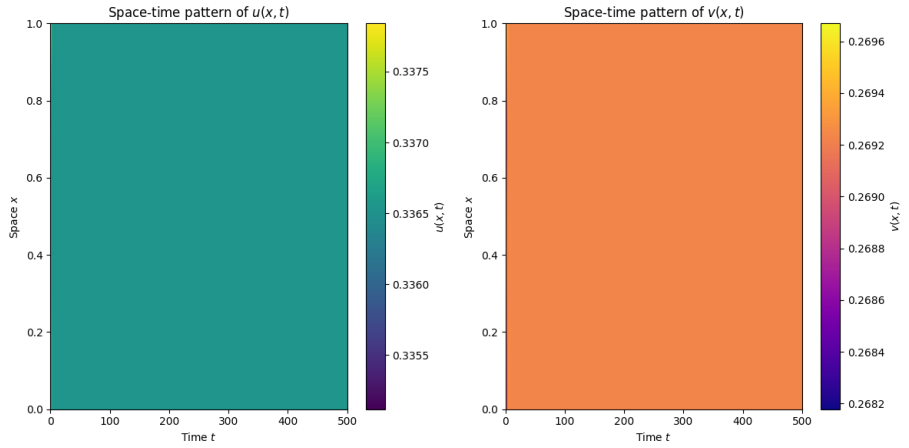

Figure 5.2: Absence of pattern formation in system (2.2) under self-diffusion with $d_{11} = 0.005$ and $d_{22} = 0.01$.

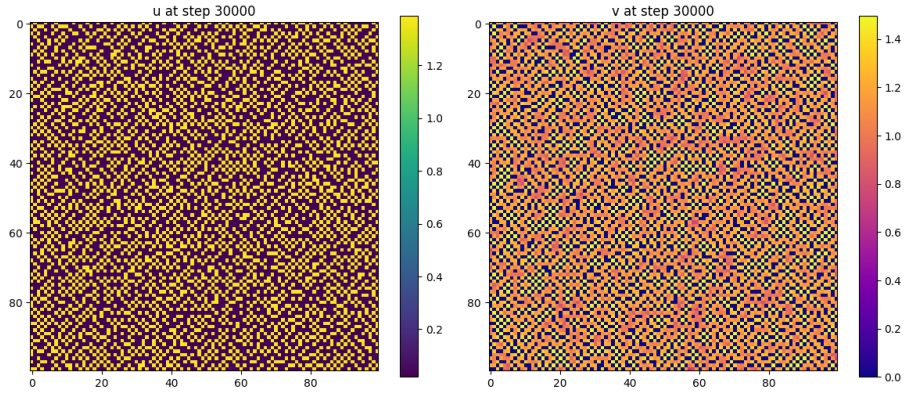

Figure 5.3: Turing pattern for $d_{11} = 0.01$, $d_{12} = 0.004$, $d_{21} = 1.2$, $d_{22} = 0.7$.

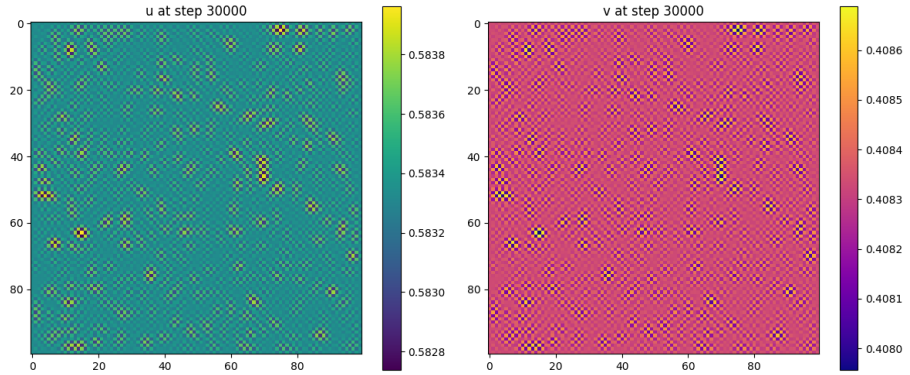

Figure 5.4: Turing pattern for $d_{11} = 0.01$, $d_{12} = 0.004$, $d_{21} = 0.4895$, $d_{22} = 0.7$.

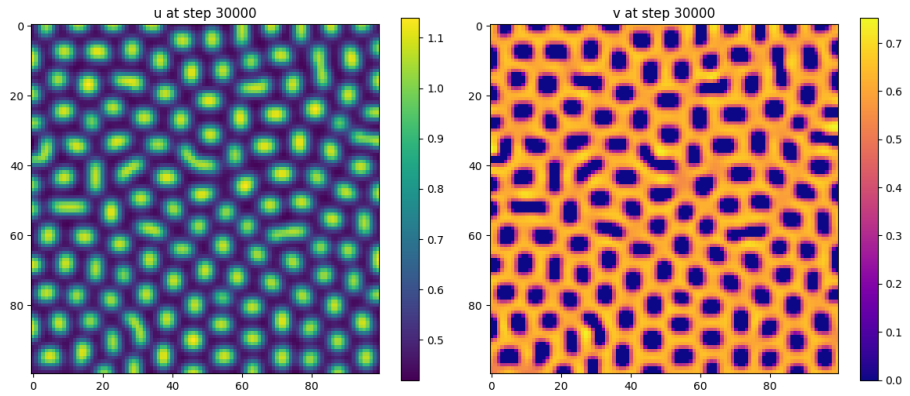

Figure 5.5: Mixed Turing pattern exhibiting both stripes and spots for $d_{11} = 1$, $d_{12} = 0.01$, $d_{21} = 3.4$, $d_{22} = 1.1$.

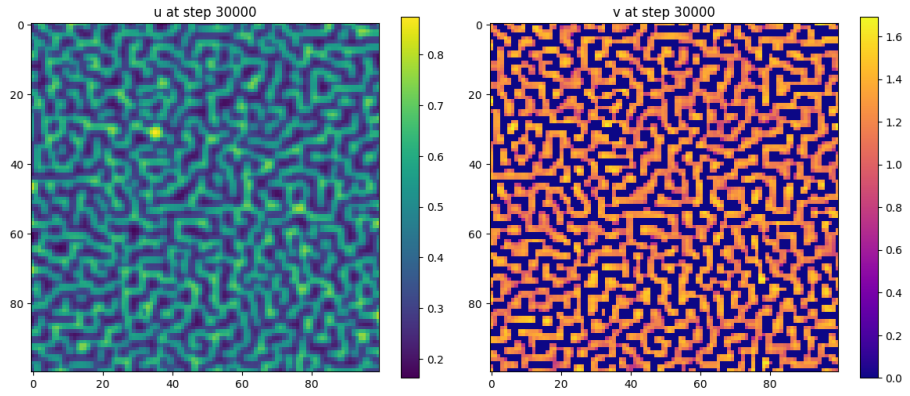

Figure 5.6: Turing stripe pattern, for $d_{11} = 1$, $d_{12} = 0.01$, $d_{21} = 12$, $d_{22} = 1.1$.

5.2 Non-autonomous system

To illustrate Theorem 4.2, we present a numerical example for model (2.4). Let $b = 0.6$, $k = 50$, $\mu = 1$, $\omega = \frac{2\pi}{T} = 1$, $T = 2\pi$,

$$a(t) = 0.3\big(1 + 0.4\sin t\big), \quad h(t) = 0.04\big(1 + 0.4\sin(t + \tfrac{\pi}{3})\big), \quad r(t) = 1.6\big(1 + 0.3\sin t\big)\,.$$

For these choices we have the bounds

$$M_1 = 48.6538, \qquad M2 = 12.2607, \qquad M3 = 47.6354, \qquad M4 = 5.1446\,.$$

Consequently, the assumptions for Theorem 4.2 hold, and system (2.4) has at least one periodic solution, see Figure 5.7.

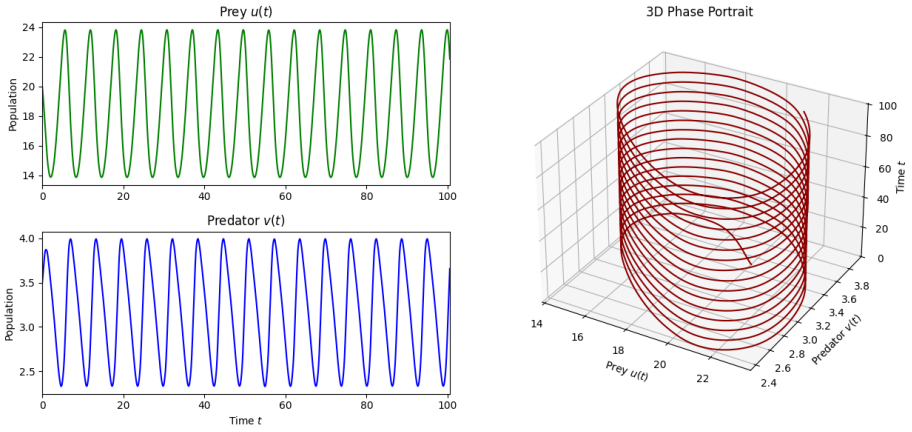

Figure 5.7: Periodic dynamics for system (2.4) with initial condition $(20, 3.5)$.

6 Sensitivity analysis

In this section we quantify how variations in input parameters affect model outputs, identifying the most influential parameters [16]. To evaluate the impact of model parameters on predator–prey dynamics, we performed SA using Latin Hypercube Sampling (LHS) combined with Partial Rank Correlation Coefficients (PRCCs). Each of the six parameters (a, b, h, k, μ, r) was varied within $\pm 25\%$ of its nominal value.

The resulting PRCC values, ranging from -1 to 1, are visualized as bar charts. Figure 6.1 shows the results for these parameters. It is evident that the most influential parameters are a for prey and r for predator, as their PRCC values exceed ± 0.5.

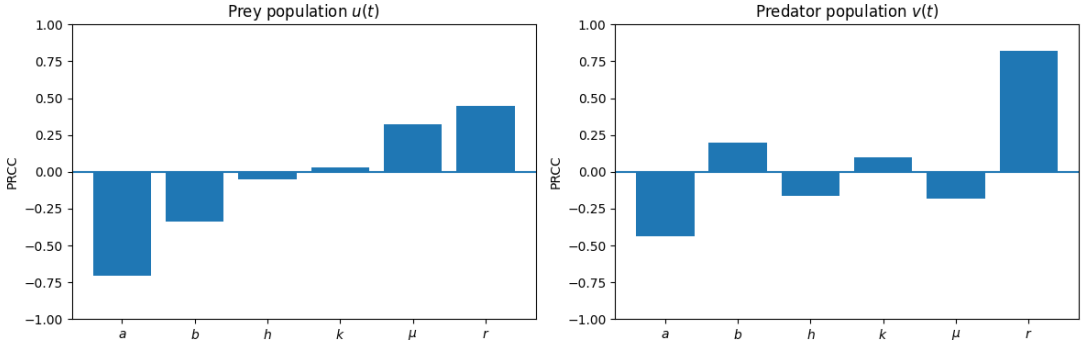

Figure 6.1: Estimated parameter sensitivities for prey (left) and predator (right) populations with respect to parameters $a = 0.6$, $b = 0.5$, $h = 0.2$, $k = 10.0$, $\mu = 0.4$, and $r = 1.0$.

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