

Investigating the Stochastic Dynamics of a Predator-Prey System, with Fourier Applications

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We consider the following system of ordinary differential equations describing the interactions between a population of predators $h(t)$ and prey $p(t)$:

$$\frac{dp(t)}{dt} = \gamma_p p(t) \left(1 - \frac{p(t)}{K}\right) - \mu_p h(t)p(t) =: f(p(t), h(t)) \quad (1)$$

$$\frac{dh(t)}{dt} = \gamma_h p(t)h(t) - \mu_h h(t) =: g(p(t), h(t)). \quad (2)$$

Here, γ_p , μ_p , γ_h , and μ_h are model parameters, and t represents time.

In equation (1), the term $\gamma_p p(1 - \frac{p}{K})$ represents the logistic growth of the prey population, with intrinsic growth rate γ_p (representing the natural births of the prey) and carrying capacity K . The interaction term $-\mu_p hp$ has coefficient μ_p , representing the rate at which a predator kills a prey. The negative sign is to indicate that this term will decrease the density of prey.

In equation (2), the interaction term $\gamma_h ph$ represents the 'births' of the predator made possible by feeding off of prey, with birth rate γ_h . The term $-\mu_h h$ demonstrates the natural death of predators, with rate μ_h . Again we note the negative sign to indicate that deaths will diminish the predator population. [1]

1 Linear Stability Analysis

We identify the steady states of the system:

$$\begin{aligned} \frac{dp(t)}{dt} &= \gamma_p p(t) \left(1 - \frac{p(t)}{K}\right) - \mu_p h(t)p(t) = 0 \\ h \left(1 - \frac{\gamma_h}{\mu_h} p\right) &= 0 \end{aligned}$$

Therefore, $h = 0$ or $p = \frac{\mu_h}{\gamma_h}$.

$$\begin{aligned} \frac{dh(t)}{dt} &= \gamma_h p(t)h(t) - \mu_h h(t) = 0 \\ \gamma_p p \left(1 - \frac{p}{K}\right) &= \mu_p hp \end{aligned}$$

Substituting $h = 0$, we find

$$\begin{aligned} \gamma_p p \left(1 - \frac{p}{K}\right) &= 0 \\ p^2 - Kp &= 0 \end{aligned}$$

where we assumed $\gamma_p \neq 0$. Further assumptions we will be making throughout the exercises is that all parameters, unless stated otherwise, are strictly positive. The solutions to the above equation are $p = 0$ or $p = K$.

Thus $(0, 0)$ is the extinction steady state and $(K, 0)$ is the predator extinction steady state.

Substituting $p = \frac{\mu_h}{\gamma_h}$ into the rearranged steady state solution equation for the predator dynamics we get

$$\begin{aligned}\gamma_p \frac{\mu_h}{\gamma_h} \left(1 - \frac{\mu_h}{K\gamma_h}\right) &= h \frac{\mu_p \mu_h}{\gamma_h} \\ h &= \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\end{aligned}$$

where we have assumed that $\frac{\mu_h}{\gamma_h} \neq 0$ in our rearranging.

Therefore the coexistence steady state is found to be $\left(\frac{\mu_h}{\gamma_h}, \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\right)$.

Calculate the Jacobian: $J = \begin{bmatrix} \frac{\partial f}{\partial p} & \frac{\partial f}{\partial h} \\ \frac{\partial g}{\partial p} & \frac{\partial g}{\partial h} \end{bmatrix}$, where $f(p, h) := \frac{dp}{dt}$ and $g(p, h) := \frac{dh}{dt}$.

We calculate the components of the Jacobian, using equations (1) and (2), to be:

- $\frac{\partial f}{\partial p} = \gamma_p - \frac{2\gamma_p}{K}p - \mu_p h$
- $\frac{\partial f}{\partial h} = -\mu_p p$
- $\frac{\partial g}{\partial p} = \gamma_h h$
- $\frac{\partial g}{\partial h} = \gamma_h p - \mu_h$

Next, we evaluate the Jacobian at the steady states, and calculate the characteristic polynomial from $\det(J - \lambda I) = 0$ to find the eigenvalues of J.

For the extinction steady state, $(0, 0)$:

$$\begin{aligned}J(0, 0) &= \begin{bmatrix} \gamma_p & 0 \\ 0 & -\mu_h \end{bmatrix}, \\ \det(J - \lambda I) &= 0, \\ (\gamma_p - \lambda)(-\mu_h - \lambda) &= 0, \\ \lambda^2 - \lambda(\gamma_p - \mu_h) + \gamma_p \mu_h &= 0.\end{aligned}$$

We can read off the trace and determinant: $\text{tr}(J(0, 0)) = \gamma_p - \mu_h$, $\det(J(0, 0)) = -\gamma_p \mu_h$. Assuming positive parameters results in a negative determinant, and so we classify $(0, 0)$ to be a *saddle point*, which is unstable.

For the predator extinction steady state, $(K, 0)$:

$$\begin{aligned}J(K, 0) &= \begin{bmatrix} -\gamma_p & -\mu_p K \\ 0 & \gamma_h K - \mu_h \end{bmatrix}, \\ \det(J - \lambda I) &= 0, \\ (-\gamma_p - \lambda)(-\gamma_h K - \mu_h - \lambda) &= 0, \\ \lambda^2 - \lambda(\gamma_h K - \mu_h - \gamma_p) + (\gamma_p \mu_h - \gamma_p \gamma_h K) &= 0.\end{aligned}$$

We can read off the trace and determinant:

- $tr(J(K, 0)) = -\gamma_p + (\gamma_h K - \mu_h)$,
- $det(J(K, 0)) = -\gamma_p(\gamma_h K - \mu_h)$.

We see that for $\gamma_h K > \mu_h$, the determinant becomes negative, and $(K, 0)$ becomes a saddle point. Conversely, for $\gamma_h K < \mu_h$ the determinant will be positive and the trace negative, implying that both eigenvalues $\lambda_{1,2}$ are real and negative. Therefore making the predator extinction point a stable node.

For the coexistence steady state, $\left(\frac{\mu_h}{\gamma_h}, \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\right)$:

$$J\left(\frac{\mu_h}{\gamma_h}, \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\right) = \begin{bmatrix} -\frac{\gamma_p}{K} \frac{\mu_h}{\gamma_h} & -\mu_p \frac{\mu_h}{\gamma_h} \\ \frac{\gamma_h \gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right) & 0 \end{bmatrix}.$$

We can read off the trace and determinant:

- $tr\left(J\left(\frac{\mu_h}{\gamma_h}, \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\right)\right) = -\frac{\gamma_p}{K} \frac{\mu_h}{\gamma_h}$,
- $det\left(J\left(\frac{\mu_h}{\gamma_h}, \frac{\gamma_p}{\mu_p} \left(1 - \frac{\mu_h}{K\gamma_h}\right)\right)\right) = \mu_h \gamma_p \left(1 - \frac{\mu_h}{K\gamma_h}\right)$

Once again, under the assumption that all of our parameters are positive, the trace of this steady state becomes negative. If $\gamma_h K > \mu_h$, our determinant is positive, resulting in our coexistence point being a stable node. However, if $\gamma_h K < \mu_h$ our determinant becomes negative, making negative and our steady state unstable.

In summary, the long-term behaviour of the system (assuming non-zero initial population sizes of p and h) is as follows:

- For $\gamma_h K > \mu_h$, we would expect the predator and prey populations to converge to the (stable) coexistence steady state.
- For $\gamma_h K < \mu_h$ the predator extinction point is stable, implying that introduction of predators into the system is not a sustainable approach. As the predator population decay to extinction, the prey population will converge to their carrying capacity K .

2 Deterministic Simulations

For the parameter combination $\gamma_p = 1$, $\mu_p = 0.01$, $\gamma_h = 1$, $\mu_h = 100$, $K = 200$, and the initial condition $p(0) = 100$, $h(0) = 45$, we use our calculations from the previous exercise to calculate the exact values of the steady states and inequality which determines the behaviour of the system.

The parameters reveal that $\gamma_h K = 1 \times 200$, which is larger than $\mu_h = 100$, hence:

- The predator extinction point, $(100, 0)$ is unstable (specifically, it is a saddle point).
- The coexistence point, which is calculated to be $(100, 50)$, is a stable node.

We see in Figure 1 that our simulations agree with our numerical approximations.

3 Stochastic Simulations

Next, we investigate the effect of stochastic noise on the system dynamics. Specifically, we extend equations (1) and (2) into stochastic differential equations by introducing noise terms of strength α_p and α_h , i.e.,

$$\frac{dp(t)}{dt} = \gamma_p p(t) \left(1 - \frac{p(t)}{K}\right) - \mu_p h(t) p(t) + \alpha_p \xi_p, \quad (3)$$

$$\frac{dh(t)}{dt} = \gamma_h p(t) h(t) - \mu_h h(t) + \alpha_h \xi_h. \quad (4)$$

For SDEs described in equations (3) and (4), our first aim is to identify the possible dynamics of this system numerically, using a time step of $\Delta t = 0.0001$ and $\alpha_p = \alpha_h = 5$. Use reflecting boundary conditions at $p = 0$ and $h = 0$ to ensure non-negative population sizes.

See Figures 2 and 3 for the simulations of the predator-prey dynamics with the stochastic noise, as described by equations (3) and (4).

4 Linearisation

Assuming that (p_0, h_0) is the non-zero steady state of the system and that there are small perturbations $\delta p(t)$ and $\delta h(t)$ such that

$$\begin{aligned} p(t) &= p_0 + \delta p(t), \\ h(t) &= h_0 + \delta h(t). \end{aligned}$$

Also assuming that $\delta p(t) \ll 1$ and $\delta h(t) \ll 1$, we linearize the system of equations (3) and (4) to identify a linear system of SDEs of the form

$$\begin{aligned} \frac{d\delta p(t)}{dt} &= \dots, \\ \frac{d\delta h(t)}{dt} &= \dots \end{aligned}$$

Firstly, we initialise the steady state conditions by evaluating $\frac{dp(t)}{dt}$ and $\frac{dh(t)}{dt}$ at the steady state (p_0, h_0) [2]:

$$\begin{aligned} \frac{dp}{dt} &= \gamma_p p_0 \left(1 - \frac{p_0}{K}\right) - \mu_p h_0 p_0 = 0 \\ \frac{dh}{dt} &= \gamma_h p_0 h_0 - \mu_h h_0 = 0. \end{aligned}$$

Linearising our prey dynamics:

$$\begin{aligned} LHS : \frac{dp(t)}{dt} &= \frac{d}{dt}(p_0 + \delta p(t)) = \frac{d\delta p(t)}{dt} \\ RHS : \gamma_p(p_0 + \delta_p) &\left(1 - \frac{p_0 + \delta_p}{K}\right) - \mu_p(h_0 + \delta_h)(p_0 + \delta_p) + \alpha_p \xi_p \\ RHS : \gamma_p p_0 + \gamma_p \delta_p &- \frac{\gamma_p p_0^2 + 2\gamma_p p_0 \delta_p + \gamma_p \delta_p^2}{K} - \mu_p h_0 p_0 - \mu_p \delta_p h_0 - \mu_p p_0 \delta_h - \mu_p \delta_h \delta_p + \alpha_p \xi_p \end{aligned}$$

Applying the condition that non-linear terms of small δ_h and δ_p will be negligibly small:

$$\begin{aligned} RHS : \gamma_p p_0 - \frac{\gamma_p p_0^2}{K} &- \mu_p p_0 h_0 + \gamma_p \delta_p - \frac{2\gamma_p \delta_p p_0}{K} - \mu_p \delta_h p_0 - \mu_p p_0 \delta_h + \alpha_p \xi_p \\ RHS : \gamma_p p_0 \left(1 - \frac{p_0}{K}\right) &- \mu_p p_0 h_0 + \delta_p \left(\gamma_p \left(1 - \frac{2p_0}{K}\right) - \mu_p h_0\right) - \delta_h \mu_p p_0 + \alpha_p \xi_p \end{aligned}$$

Noticing the steady state condition in the above term, we are able to conclude that

$$\frac{d\delta p(t)}{dt} = \delta_p \left(\gamma_p \left(1 - \frac{2p_0}{K}\right) - \mu_p h_0\right) - \delta_h \mu_p p_0 + \alpha_p \xi_p \quad (7)$$

Linearising our predator dynamics:

$$LHS : \frac{dh(t)}{dt} = \frac{d}{dt}(h_0 + \delta_h(t)) = \frac{d\delta_h(t)}{dt}$$

$$RHS : \gamma_h(p_0 + \delta_p)(h_0 + \delta_h) - \mu_h(h_0 + \delta_h) + \alpha_h \xi_h$$

$$RHS : \gamma_h p_0 h_0 - \mu_h h_0 + \gamma_h \delta_p h_0 + \gamma_h \delta_h p_0 - \mu_h \delta_h + \gamma_h \delta_p \delta_h + \alpha_h \xi_h$$

Again, cancelling the non-linear δ_h and δ_h terms and applying the steady state condition, we are left with

$$\frac{d\delta_h(t)}{dt} = \delta_p \gamma_h h_0 + \delta_h(\gamma_h p_0 - \mu_h) + \alpha_h \xi_h \quad (8)$$

5 Transformation to Fourier Space

We solve the system of equations (7) and (8) in Fourier space. To do so, we apply Fourier transforms to each side of the equation, using the notation

$$\tilde{\xi}_p = \mathcal{F}(\xi_p), \quad (9)$$

$$\tilde{\xi}_h = \mathcal{F}(\xi_h), \quad (10)$$

where $\mathcal{F}(\cdot)$ denotes the Fourier transform. We shall express the Fourier transforms of $\delta p(t)$ and $\delta h(t)$ in terms of $\tilde{\xi}_p$ and $\tilde{\xi}_h$.

We must make use of the following equation [3]

$$F\left(\frac{d}{dx}f\right) = i\omega f(x).$$

We can now apply the Fourier transformations to the left- and right-hand sides of equations (7) and (8).

The Fourier transformation of the prey dynamics are:

$$LHS : F\left(\frac{d}{dt}\delta_p(t)\right) = i\omega \tilde{\delta}_p$$

$$RHS : \tilde{\delta}_p \left(\gamma_p \left(1 - \frac{2p_0}{K} \right) - \mu_p h_0 \right) - \tilde{\delta}_h \mu_p p_0 + \alpha_p \tilde{\xi}_p$$

Equate LHS and RHS such that

$$i\omega \tilde{\delta}_p = X_p \tilde{\delta}_p + Y_p \tilde{\delta}_h + \alpha_p \tilde{\xi}_p,$$

where we define the following parameters; $X_p := (\gamma_p (1 - \frac{2p_0}{K}) - \mu_p h_0)$, $Y_p := -\mu_p p_0$.

Similarly, the Fourier transformation of the predator dynamics are as follows:

$$LHS : F\left(\frac{d}{dt}\delta_h(t)\right) = i\omega \tilde{\delta}_h$$

$$RHS : \tilde{\delta}_p \gamma_h h_0 + \tilde{\delta}_h (\gamma_h p_0 - \mu_h) + \alpha_h \tilde{\xi}_h$$

Equating LHS and RHS such that

$$i\omega \tilde{\delta}_h = X_h \tilde{\delta}_p + Y_h \tilde{\delta}_h + \alpha_h \tilde{\xi}_h$$

where we define the parameters; $X_h := \gamma_h h_0$, $Y_h := \gamma_h p_0 - \mu_h$.

Rearranging both equations we are able to find expression for $\tilde{\xi}_p$ and $\tilde{\xi}_h$ in terms of $\tilde{\delta}_p$ and $\tilde{\delta}_h$ and the parameters:

$$\begin{aligned}\tilde{\delta}_p(i\omega - X_p) - \tilde{\delta}_h Y_h &= \alpha_p \tilde{\xi}_p \\ -X_h \tilde{\delta}_p + \tilde{\delta}_h(i\omega - Y_h) &= \alpha_h \tilde{\xi}_h.\end{aligned}$$

Writing this in matrix form:

$$\begin{bmatrix} i\omega - X_p & -Y_p \\ -X_h & i\omega - Y_h \end{bmatrix} \begin{bmatrix} \tilde{\delta}_p \\ \tilde{\delta}_h \end{bmatrix} = \begin{bmatrix} \alpha_p \tilde{\xi}_p \\ \alpha_h \tilde{\xi}_h \end{bmatrix},$$

where we shall define the matrix $A := \begin{bmatrix} i\omega - X_p & -Y_p \\ -X_h & i\omega - Y_h \end{bmatrix}$.

To rearrange this matrix equation in order to find expressions for $\tilde{\delta}_p$ and $\tilde{\delta}_h$, we must multiply both sides by the inverse of A . First, we find the determinant:

$$\det(A) = (i\omega - X_p)(i\omega - Y_h) - X_h Y_p$$

For the assumptions made about the parameters which make up X_p, Y_p, X_h , and Y_h , we conclude that the determinant of A is non-zero for any non-trivial solution ω such that the inverse of A can be calculated.

The matrix equation rearranges to become:

$$\begin{bmatrix} \tilde{\delta}_p \\ \tilde{\delta}_h \end{bmatrix} = \frac{1}{\det(A)} \begin{bmatrix} i\omega - Y_h & Y_p \\ X_h & i\omega - X_p \end{bmatrix} \begin{bmatrix} \alpha_p \tilde{\xi}_p \\ \alpha_h \tilde{\xi}_h \end{bmatrix}.$$

Hence, the Fourier transforms of $\delta_p(t)$ and $\delta_h(t)$ can be expressed as

$$\begin{aligned}\tilde{\delta}_p(\omega) &= \frac{1}{\det(A)} \left((i\omega - Y_h) \alpha_p \tilde{\xi}_p + Y_p \alpha_h \tilde{\xi}_h \right) \\ \tilde{\delta}_h(\omega) &= \frac{1}{\det(A)} \left(X_h \alpha_p \tilde{\xi}_p + (i\omega - X_p) \alpha_h \tilde{\xi}_h \right)\end{aligned}$$

6 The Power Spectrum

It is a given that the power spectrum of a stochastic process is defined as

$$S(\omega) = \lim_{T \rightarrow \infty} \frac{1}{2T} \mathbb{E}(X(\omega) X^*(\omega)), \quad (11)$$

where $X(\omega)$ is the finite-time Fourier transform of a sample path of the process, i.e.,

$$X(\omega) = \frac{1}{\sqrt{2\pi}} \int_{-T}^T X(t) e^{i\omega t} dt, \quad (12)$$

and the notation $*$ denotes complex conjugation.

Importantly, the finite-time Fourier transform of the independent Gaussian white noises ξ_h and ξ_p fulfils

$$\mathbb{E}(\tilde{\xi}_p \tilde{\xi}_p^*) = 2T = \mathbb{E}(\tilde{\xi}_h \tilde{\xi}_h^*), \quad (13)$$

$$\mathbb{E}(\tilde{\xi}_p \tilde{\xi}_h) = \mathbb{E}(\tilde{\xi}_p \tilde{\xi}_h^*) = 0. \quad (14)$$

Using the relationships (13), (14), (11), and the results from the Fourier transformations, we calculate the power spectrum $S_p(\omega)$ of the linearized copy number fluctuations of the prey.

Using equation (11), to find the power spectrum $S_p(\omega)$ we first need to calculate

$$\tilde{\delta}_p \tilde{\delta}_p^* = \frac{1}{\det(A)\det^*(A)} \left((i\omega - Y_h)\alpha_p \tilde{\xi}_p + Y_p \alpha_h \tilde{\xi}_h \right) \left((-i\omega - Y_h)\alpha_p \tilde{\xi}_p^* + Y_p \alpha_h \tilde{\xi}_h^* \right).$$

Using the knowledge that, for a complex number z , $zz^* = |z|^2$, we expand and obtain

$$\tilde{\delta}_p \tilde{\delta}_p^* = \frac{1}{|\det(A)|^2} \left(\alpha_p^2 (i\omega - Y_h)(-i\omega - Y_h) \tilde{\xi}_p \tilde{\xi}_p^* + \alpha_h^2 Y_p^2 \tilde{\xi}_h \tilde{\xi}_h^* + (i\omega - Y_h)Y_p \alpha_p \alpha_h \tilde{\xi}_p \tilde{\xi}_h^* + (-i\omega - Y_h)Y_p \alpha_p \alpha_h \tilde{\xi}_p^* \tilde{\xi}_h \right).$$

Taking the expectation, we are able to omit the final two terms using equation (13) ($E(\tilde{\xi}_p \tilde{\xi}_h^*) = 0$) and the conjugate of equation (13) ($E(\tilde{\xi}_p^* \tilde{\xi}_h) = 0^* = 0$). We also use the properties from equation (14) ($E(\tilde{\xi}_p \tilde{\xi}_p^*) = E(\tilde{\xi}_h \tilde{\xi}_h^*) = 2T$) to further simplify the expression

$$E(\tilde{\delta}_p \tilde{\delta}_p^*) = \frac{1}{|\det(A)|^2} (2T\alpha_p^2(\omega^2 + Y_h^2) + 2T\alpha_h^2 Y_p^2).$$

Finally, we are able to put this expression into equation (11) to calculate the power spectrum of the linearised copy number fluctuations of the prey:

$$S_p(\omega) = \lim_{T \rightarrow \infty} \frac{1}{2T} \mathbb{E}(\tilde{\delta}_p(\omega) \tilde{\delta}_p^*(\omega)) = \lim_{T \rightarrow \infty} \frac{\alpha_p^2(\omega^2 + Y_h^2) + \alpha_h^2 Y_p^2}{|\det(A)|^2}.$$

Hence

$$S_p(\omega) = \frac{\alpha_p^2(\omega^2 + Y_h^2) + \alpha_h^2 Y_p^2}{|\det(A)|^2},$$

where all parameters have been defined above.

For the power spectrum shown in Figure 4, we are able to see a peak at $\omega := \omega_0 = 6.7094$, for the power spectrum of value $S_p(\omega_0) = 126.1956$. The value ω_0 represents the the strongest frequency, i.e. the strongest rate of oscillations in our predator-prey dynamics due to stochastic effects.

$T_p = \frac{2\pi}{\omega_0}$ represents the period of the oscillations at the highest frequency ω_0 . In other words, T_p is the time it takes for the predator and prey populations to complete one full cycle of oscillations.

A Figures

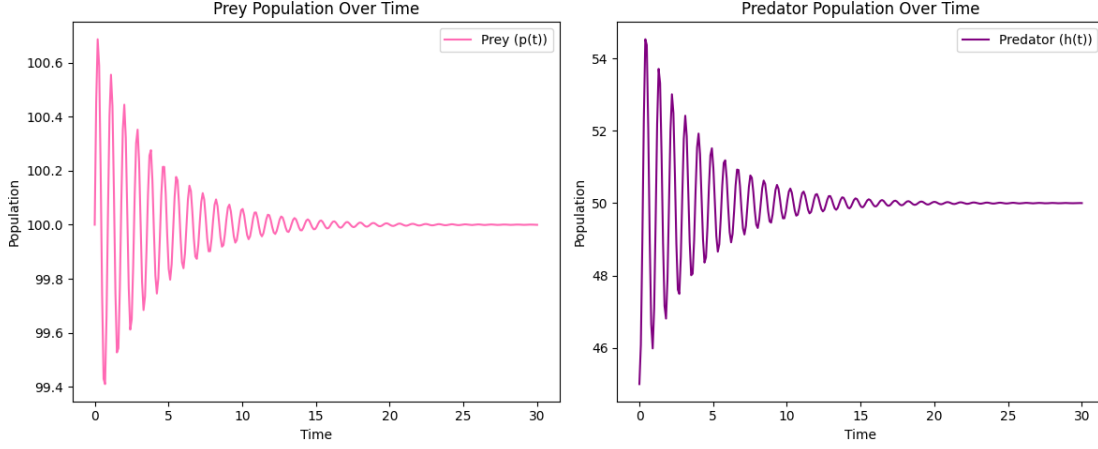


Figure 1: As expected, we see on the left that the prey population dynamics converge to a stable point at $p(t) = 100$. Similarly, on the right the predator population dynamics converge at the same time step ($t = 30$) to a stable point at $h(t) = 50$. Therefore we can see that our predator-prey system converges to the coexistence steady state $(100, 50)$, and thus agrees with our numerical calculations.

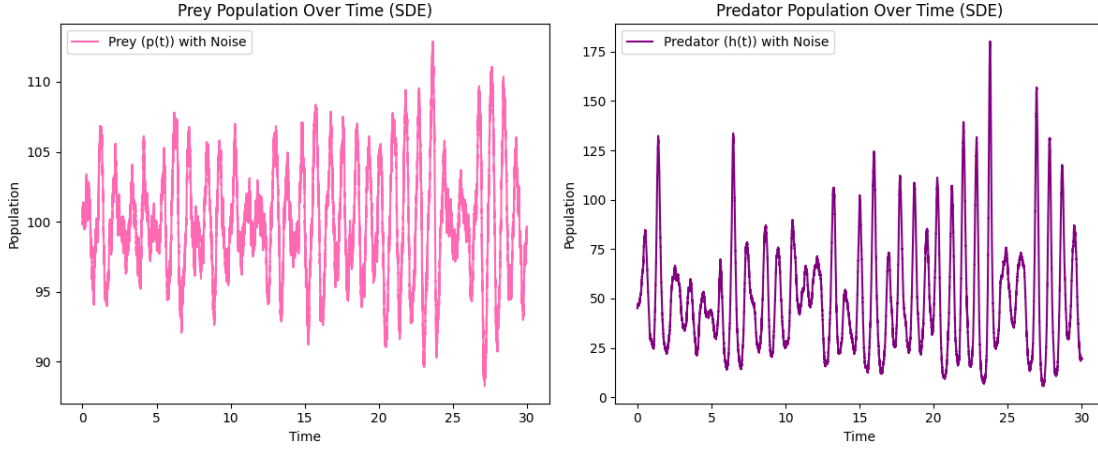


Figure 2: On the left we have simulated the prey dynamics with added stochasticity. Similarly, on the right we have simulated the predator dynamics with added stochasticity. Unlike in the simulations of the deterministic cases (see Figure 1), we see that our predator-prey populations do not converge to a stable point. Instead, they oscillate around the stable coexistence steady state of the deterministic case.

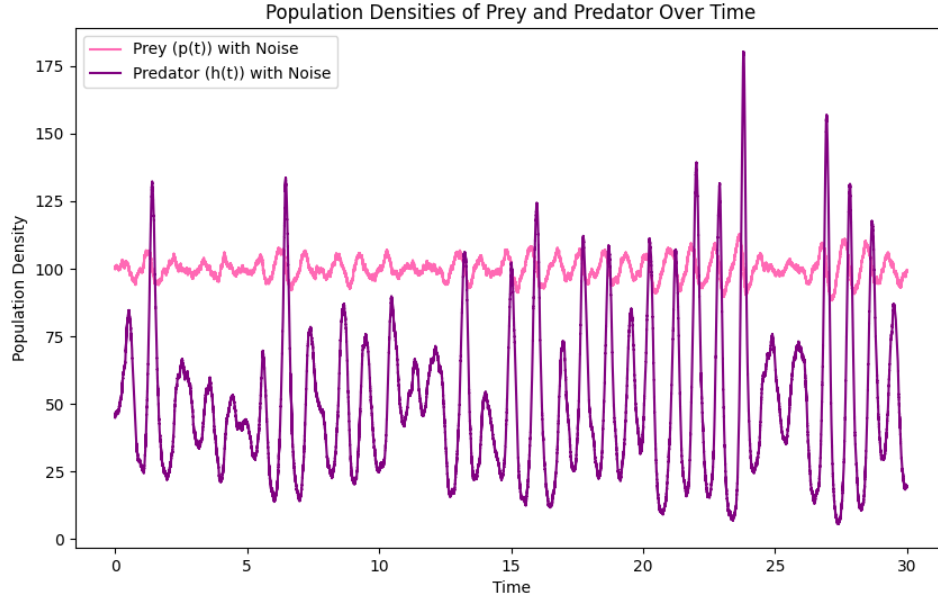


Figure 3: By plotting both prey and predator population densities on the same y-axis, we are able to see the difference in the sizes of their oscillations. Whilst the prey population oscillates very closely to its deterministic steady state ($p(t) = 100$), the oscillations of the predator population appear to be much larger.

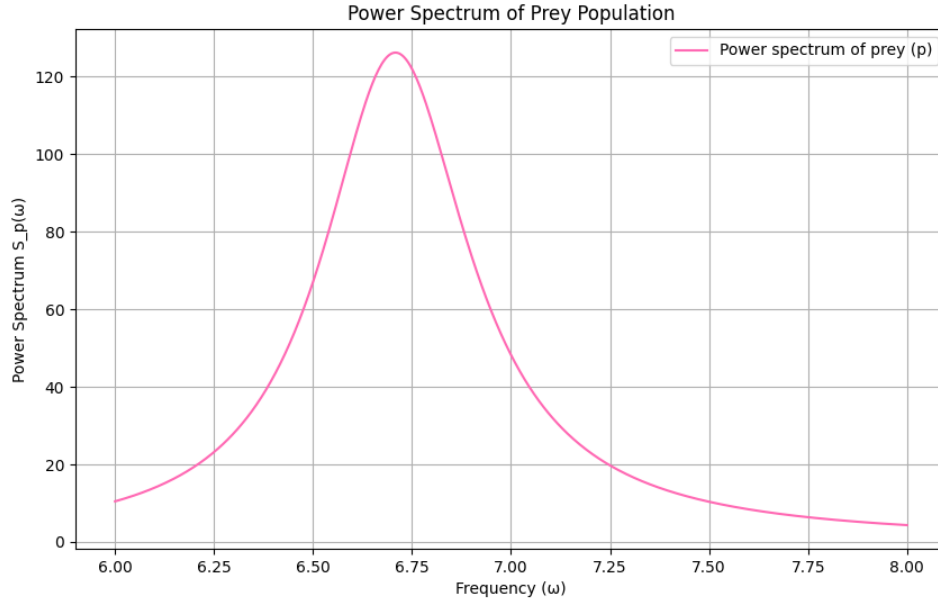


Figure 4: The power spectrum $S_p(\omega)$ of the linearised copy number of fluctuations of the prey is shown in the interval $\omega \in [6, 8]$, with the peak $(\omega_0, S_P(\omega_0)) = (6.7, 126.2)$.

References

- [1] J.D. Murray, *Mathematical Biology I, An Introduction*, Chapter 3.
- [2] J. Kursawe, *Linear Stability Analysis - Reminder*.
- [3] J. Kursawe, *Fourier analysis of Stochastic processes*.