

Chapter 11

Predator-prey Dynamics

We have been mostly working on one variable systems, except for a few examples in the exercises. Here we take an example topic that (almost) everything we have learned so far can be used to analyze the system, but for a two-variable system. The chosen example is the *predator-prey dynamics*, where we consider a population of agents - for example, hare that grows and is eaten by another agent, for example, lynx, that needs to eat hares to grow, while they can die. Interestingly, it has been found that the population of such a system sometimes shows an oscillation, as observed by MacLulich in 1937 (Fig. 11.1). What is the mechanism of the oscillation of the number of preys $N(t)$ and predators $M(t)$? There are many possibilities - and here, we learn one of the possible mechanisms, where the stochasticity of the system plays an important role. The content of this chapter is based on ref. [24] with small modifications.

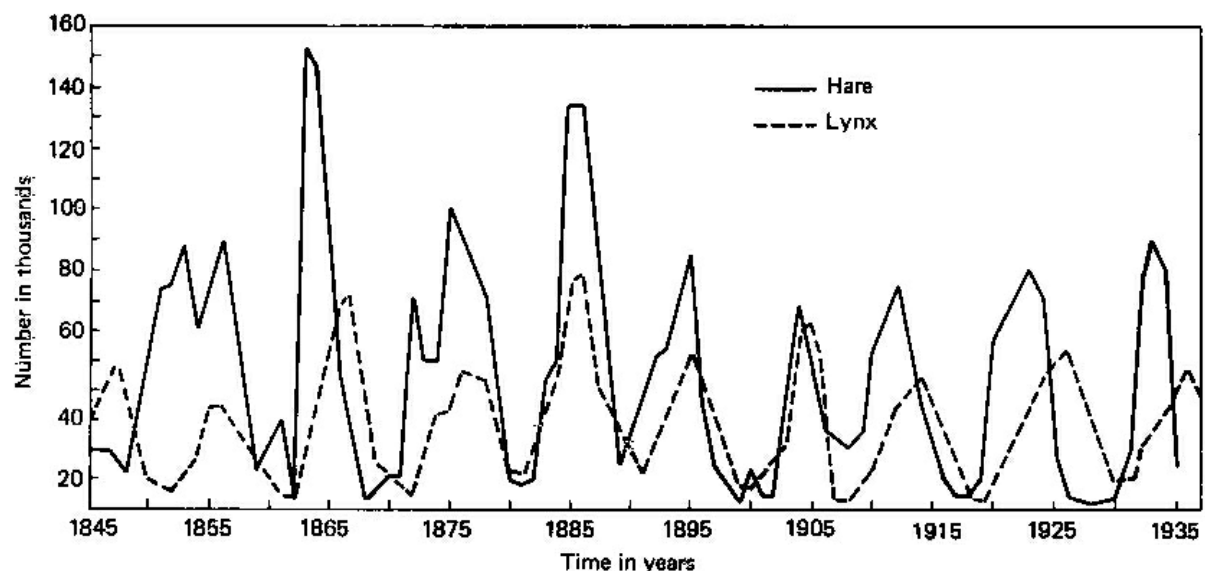


Figure 9-3. Changes in the abundance of the lynx and the snowshoe hare, as indicated by the number of pelts received by the Hudson's Bay Company. This is a classic case of cyclic oscillation in population density. (Redrawn from MacLulich 1937.)

Figure 11.1: Predator-prey oscillation.

11.1 Agent-based rule of predator-prey interaction

Let us consider $N(t)$ preys and $M(t)$ predators in the system. For later convenience, let me express preys as A and Predator as B , and define each “reaction” of growth and death.

Prey growth For simplicity, we assume that one prey can “double” at the rate α per prey. If that is the only rule, it means $A \rightarrow 2A$ at a constant rate, but then A will keep increasing exponentially if there is no B to kill it. So we also assume that there is a maximum integer number K of the preys that the world can support - this can be due to the limit of the available food for them. We assume that this limit kicks in as a form of *logistic growth*, i.e., the rate of $A \rightarrow 2A$ per prey is given as $\alpha \cdot (1 - N(t)/K)$. In other words,

$$N \rightarrow N + 1 \quad \text{at the rate} \quad \alpha \cdot N(1 - N/K).$$

Note that, for this model, we limit the range of N being $0 \leq N \leq K$, which makes the rate defined above always non-negative. Because N can increase only one at a time and K is an integer, when N hits exactly K the growth rate becomes zero, and hence N cannot exceed K as long as the initial condition satisfies $N \leq K$.

Prey death by predation We use the simplest form here, too, where we assume that when the two meet, there is a probability that a prey is lost, i.e., $A + B \rightarrow B$. The probability of one prey meeting a predator depends on the predator’s density. Here, let us use the carrying capacity K as the “volume” of the system since it is natural that K is proportional to the total system size. Namely, we consider N/K as the prey density and M/K as the predator density. We then set the rule for the prey death by predation using a constant β as

$$N \rightarrow N - 1 \quad \text{at the rate} \quad \beta \cdot N \cdot \frac{M}{K}.$$

Predator growth by eating a prey Predator can grow only by eating preys. If it is lynx, it probably needs to eat a certain number of the preys before it “doubles”. Keeping track of predation event however complicates the problem, so, for now, we make a very simple assumption: Once in a while, upon a predation event, a prey dies and the predator doubles, i.e., $A + B \rightarrow 2B$, with some rate per predation event. Then, by using a new constant γ , we have

$$M \rightarrow M + 1 \quad \text{and} \quad N \rightarrow N - 1 \quad \text{at the rate} \quad \gamma \cdot M \cdot \frac{N}{K}.$$

Predator death Predator dies, and here again, for simplicity, we assume it happens at a constant rate of δ per predator. This gives

$$M \rightarrow M - 1 \quad \text{at the rate} \quad \delta \cdot M.$$

These rules define the dynamics. It is left for exercise to perform a Gillespie simulation of this model. Does the model show interesting behaviour?

11.2 Rate equations: Deterministic Lotoka-Volterra model with logistic growth for prey

To have some insight into the system’s dynamics, let us think about the rate equation, i.e., the deterministic equation to describe the behaviour of the density of prey $x = N/K$ and predator $y = M/K$ in the large system size limit ($K \rightarrow \infty$) with keeping the density constant, hence the noise is negligible. For example, for the prey, we naturally have (and can be derived by using the master equation (11.7) if you want to make sure)

$$\frac{d\langle N \rangle}{dt} = \left\langle \alpha N \left(1 - \frac{N}{K} \right) \right\rangle - \left\langle (\beta + \gamma) \cdot N \cdot \frac{M}{K} \right\rangle,$$

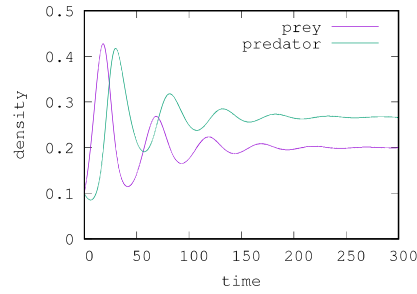


Figure 11.2: An example trajectory of the deterministic rate equation for the prey population density x and predator population density y . The parameters are $\alpha = 0.2$, $\beta = 0.1$, $\gamma = 0.5$, $\delta = 0.1$.

where the average change of N is given by the average rate of increase minus the average rate of decrease. By dividing both sides by K to convert the unit into density, and assuming that in the large system size limit, there is no noise, hence we can approximate $\langle(N/K)(M/K)\rangle$ as $\langle N/K\rangle\langle M/K\rangle = xy$ (mean-field approximation), and doing similar treatment also for $d\langle M\rangle/dt$, we get a well-studied simple deterministic model as follows:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x(1-x) - (\beta + \gamma)xy = x[\alpha(1-x) - (\beta + \gamma)y], \\ \frac{dy}{dt} &= \gamma xy - \delta y = y[\gamma x - \delta].\end{aligned}\tag{11.1}$$

The functional form of predator growth is called logistic growth, and the functional form of the predator-prey interaction is called the Lotoka-Volterra interaction.

This model has multiple fixed points (steady states). The trivial one is

$$x = 0, \quad y = 0,\tag{11.2}$$

i.e., both the predator and the prey went extinct. Let's call this the "full extinction fixed point". Another relatively easy case, which we now call the "prey-only fixed point" is

$$x = 1, \quad y = 0,\tag{11.3}$$

i.e., there is no predator, and the hare population is at the carrying capacity of the system. The last fixed point, which is probably the most interesting and we now call the "coexistence fixed point", is

$$x = \frac{\delta}{\gamma}, \quad y = \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right).\tag{11.4}$$

This coexistence solution is feasible (i.e., both densities are positive values) only if $\delta/\gamma < 1$, i.e., the prey population needed to sustain the predator is below the carrying capacity. Let's assume that this is true, so the coexistence fixed point is feasible.

Now, if we start with the system with non-zero predators and preys, where does the system go? If you know *linear stability analysis* of a dynamical system, you can perform it around the fixed points to see if they are stable. Here, we don't have time to cover the linear stability analysis, so we just look at the numerical simulation of the system at a specific parameter set in Fig. 11.2. The parameters are given in the figure caption. We see that the system shows damped oscillation to converge to the coexistence fixed point. If we perform the linear stability analysis of the feasible coexistence fixed point, it is possible to show that the coexistence fixed point is always linearly stable. This means that the rate equation never shows sustained oscillation.

11.3 Back to a stochastic system: Quasi-oscillation

11.3.1 An absorbing state

Before we go into the oscillation, let us quickly touch that the stochastic model with discrete predator and prey numbers can deal with the extinction of a species. Suppose we start a stochastic Gillespie simulation of the model, with the initial condition very close to the full extinction fixed point. For example, having one predator and one prey in the system. If you simulate the rate equation with the initial condition being very low predator and prey concentration, with the parameter presented in Fig. 11.2 you will actually find that deterministically the system will go to the coexistence fixed point. This is intuitive because, if the prey and the predator density is very low, the predator-prey interaction term (product of the two densities) is a lot smaller than the prey's exponential growth - hence the prey grows first, and eventually predator also starts to grow and they find a balance.

But think about what could actually happen. The events that can happen after the given initial condition are as follows:

- The prey increases from 1 to 2 at the rate $\alpha(1 - 1/K)$
- The prey decreases from 1 to 0 by predation at the rate β/K
- The prey decreases from 1 to 0 and the predator increases from 1 to 2 at the rate γ/K
- The predator decreases from 1 to 0 at the rate δ

So, there is a finite probability that the prey disappear to 0 in the next event. Then, the only possible next event is for the predator to disappear. In other words, there is a finite probability to hit exactly $(0, 0)$, and once the system is there, there is no way to come out of it.

A state that, once entered, cannot be left, is called an absorbing state. The full extinction state in the stochastic version of the model is an absorbing state. Even though deterministically the fixed point is unstable, in a stochastic system there is a finite probability to hit this absorbing state. Understanding how often such an event happens can be important when we are considering a small population.

In general, the rate to reach an absorbing state is often an important quantity to know for stochastic processes. The methods that have been developed to analyse the first passage problem are useful to tackle such problems.

11.3.2 Quasi-oscillation

Now, let us talk about the oscillation we have seen in the experimental data. Interestingly, if we simulate the stochastic version of the model with a finite K , we observe “sustained oscillation” even if we choose the parameter that the rate equation only shows a damped oscillation. It is fun to see this by actually programming it by yourself (exercise), but you can also see an example trajectory in Fig. 11.3 left. This behaviour could be understood better by applying the tools we have learned in this course - so let's have a look at it.

Master equation

The first step for the analytic calculation is to write a master equation for probability to have n prey and m predators at time t , $P(n, m, t)$. You can see this is a one-step process, where the value of the variables changes only one by one. For later convenience, let us define two kinds of step operators as

$$E_n^\Delta f(n, m) = f(n + \Delta, m), \quad (11.5)$$

$$E_m^\Delta f(n, m) = f(n, m + \Delta). \quad (11.6)$$

Then the master equation becomes

$$\begin{aligned} \dot{P}(n, m, t) = & (E_n^{-1} - 1) \alpha n \left(1 - \frac{n}{K}\right) P(n, m, t) + (E_n^{+1} - 1) \beta \frac{m}{K} n P(n, m, t) \\ & + (E_m^{-1} E_n^{+1} - 1) \gamma \frac{n}{K} m P(n, m, t) + (E_m^{+1} - 1) \delta m P(n, m, t). \end{aligned} \quad (11.7)$$

Note that "the predator growth by eating a prey" term has the product of two step-operators, reflecting one reaction causes a change of both N and M .

Kramers-Moyal expansion, SDE, and behaviour around the fixed point

The master equation itself is still somewhat difficult to deal with, so let's perform the Kramers-Moyal expansion. Because we have two variables, n and m , we need to expand both of them, but the expansion of the step operator is in parallel as before (see eq. (8.25)). We then get

$$\begin{aligned} \frac{\partial}{\partial t} P(n, m, t) = & \left(\sum_{k=1}^{\infty} \frac{(-1)^k}{k!} \frac{\partial^k}{\partial n^k} \right) \left[\alpha n \left(1 - \frac{n}{K} \right) P(n, m, t) \right] + \left(\sum_{k=1}^{\infty} \frac{(+1)^k}{k!} \frac{\partial^k}{\partial n^k} \right) \left[\beta \frac{m}{K} n P(n, m, t) \right] \\ & + \left[\left(1 + \sum_{k=1}^{\infty} \frac{(-1)^k}{k!} \frac{\partial^k}{\partial m^k} \right) \left(1 + \sum_{j=1}^{\infty} \frac{(+1)^j}{j!} \frac{\partial^j}{\partial n^j} \right) - 1 \right] \left[\gamma \frac{n}{K} m P(n, m, t) \right] \\ & + \left(\sum_{k=1}^{\infty} \frac{(+1)^k}{k!} \frac{\partial^k}{\partial m^k} \right) [\delta m P(n, m, t)]. \end{aligned} \quad (11.8)$$

Note the cross-terms in the γ term. By truncating the expansion up to the second order, we obtain

$$\begin{aligned} \frac{\partial}{\partial t} P(n, m, t) = & -\frac{\partial}{\partial n} \left[\left(\alpha n \left(1 - \frac{n}{K} \right) - (\beta + \gamma) \frac{m}{K} n \right) P(n, m, t) \right] + \frac{1}{2} \frac{\partial^2}{\partial n^2} \left[\left(\alpha n \left(1 - \frac{n}{K} \right) + (\beta + \gamma) \frac{m}{K} n \right) P(n, m, t) \right] \\ & -\frac{\partial}{\partial m} \left[\left(\gamma \frac{n}{K} m - \delta m \right) P(n, m, t) \right] + \frac{1}{2} \frac{\partial^2}{\partial m^2} \left[\left(\gamma \frac{n}{K} m + \delta m \right) P(n, m, t) \right] \\ & -\frac{\partial^2}{\partial m \partial n} \left[\gamma \frac{n}{K} m P(n, m, t) \right]. \end{aligned} \quad (11.9)$$

This is somewhat better - at least the flux term (the first-order derivative term) does give the flux that is consistent with what is expected from the rate equation.

It may be even easier to understand the system behaviour by rewriting this into the stochastic differential equations (SDEs). It is straightforward to show that the following Ito-type SDEs give the Fokker-Planck equation given above (exercise):

$$dN = \left[\alpha N \left(1 - \frac{N}{K} \right) - \frac{(\beta + \gamma)}{K} MN \right] dt + \sum_{k=1}^4 b_{1k}(N, M) \cdot dB_k, \quad (11.10)$$

$$dM = \left[\frac{\gamma}{K} NM - \delta M \right] dt + \sum_{k=1}^4 b_{2k}(N, M) \cdot dB_k, \quad (11.11)$$

with B_k 's are independent Wiener processes, and

$$b(N, M) = \begin{pmatrix} \sqrt{\alpha N \left(1 - \frac{N}{K} \right)} & -\sqrt{\beta N \frac{M}{K}} & -\sqrt{\gamma M \frac{N}{K}} & 0 \\ 0 & 0 & \sqrt{\gamma M \frac{N}{K}} & \sqrt{\delta M} \end{pmatrix} \quad (11.12)$$

You may wonder where the 4 noise terms and the matrix b come from. The 4 noise terms represent 4 reactions, and the matrix b_{ik} is the square root of each reaction rate times how much the component changes: $i = 1$ ($i = 2$) corresponds to the prey (predator) component, and if the k -th reaction changes N (M) by $+1$ or -1 is determining the sign.

Note that the deterministic part of eqs. (11.10) and (11.11) is equivalent to the rate equations (11.1) is we replace N/K with x and M/K with y . This set of SDEs (11.10) and (11.11) makes us view the dynamics as a deterministic equation plus noise.

We are interested in the quasi-oscillation around the coexistence fixed point. So now, let us consider N and M are actually close to the coexistence fixed point but fluctuating around it, and let us take the spirit

of the system size expansion by assuming

$$N(t) = K \frac{\delta}{\gamma} + \sqrt{K} X(t), \quad (11.13)$$

$$M(t) = K \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right) + \sqrt{K} Y(t). \quad (11.14)$$

Putting this back to the SDEs and taking the most relevant order in K (which is the term proportional to \sqrt{K} , left for advanced exercise), we get

$$dX = \left[-\frac{\alpha\delta}{\gamma} X - \frac{(\beta + \gamma)\delta}{\gamma} Y \right] dt + \sum_{k=1}^4 \tilde{b}_{1k} \cdot dB_k, \quad (11.15)$$

$$dY = \left[\frac{\alpha\gamma}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right) X \right] dt + \sum_{k=1}^4 \tilde{b}_{2k} \cdot dB_k, \quad (11.16)$$

with

$$\tilde{b} = \begin{pmatrix} \sqrt{\alpha \frac{\delta}{\gamma} \left(1 - \frac{\delta}{\gamma}\right)} & -\sqrt{\beta \frac{\delta}{\gamma} \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right)} & -\sqrt{\gamma \frac{\delta}{\gamma} \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right)} & 0 \\ 0 & 0 & \sqrt{\gamma \frac{\delta}{\gamma} \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right)} & \sqrt{\delta \frac{\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right)} \end{pmatrix} \quad (11.17)$$

Note that, if we write down the corresponding Fokker-Plank equation for the distribution of X and Y , it will be the same form as what you will get if you did the system size expansion and the linear noise approximation, and then put the coexistence fixed point for the deterministic density.

Note that the coefficients in the deterministic part of eqs. (11.15) and (11.16) are given by the Jacobian matrix J of the rate equation (11.1) at the coexistence fixed point

$$J = \begin{pmatrix} -\alpha \frac{\delta}{\gamma} & -(\beta + \gamma) \frac{\delta}{\gamma} \\ \frac{\gamma\alpha}{\beta + \gamma} \left(1 - \frac{\delta}{\gamma}\right) & 0 \end{pmatrix}. \quad (11.18)$$

So, if there is no noise term, the equation becomes a linear equation

$$\frac{d\vec{X}}{dt} = J\vec{X},$$

where

$$\vec{X} \equiv \begin{pmatrix} X \\ Y \end{pmatrix}.$$

It is straightforward to see that the solution of such a linear equation can be expressed by using the eigenvalues λ_1, λ_2 and the corresponding right eigenvectors \vec{u}_1, \vec{u}_2 as

$$\vec{X} = \sum_{j=1}^2 c_j e^{\lambda_j t} \vec{u}_j,$$

hence the eigenvalue of the Jacobian tells how the system behaves without the noise.

The eigenvalues of the Jacobian (11.18) is given by

$$\lambda_{\pm} = \frac{1}{2} \left(-\frac{\alpha\delta}{\gamma} \pm \sqrt{\left(\frac{\alpha\delta}{\gamma}\right)^2 - 4\alpha\delta \left(1 - \frac{\delta}{\gamma}\right)} \right) = \frac{\alpha\delta}{2\gamma} \left(-1 \pm \sqrt{1 - 4\frac{\gamma^2}{\alpha\delta} \left(1 - \frac{\delta}{\gamma}\right)} \right). \quad (11.19)$$

Because we consider the case $\left(1 - \frac{\delta}{\gamma}\right) > 0$ (feasible coexistence point), the real parts of both of the eigenvalues are always negative. If

$$1 - 4\frac{\gamma^2}{\alpha\delta} \left(1 - \frac{\delta}{\gamma}\right) < 0,$$

the eigenvalues are complex. If there is no noise, the trajectory will show a damped oscillation and the frequency is given by the imaginary part of the eigenvalue, i.e., $\frac{\alpha\delta}{2\gamma}\sqrt{-1 + 4\frac{\gamma^2}{\alpha\delta}\left(1 - \frac{\delta}{\gamma}\right)}/2\pi$.

This gives an intuitive explanation for quasi-cycle: Deterministically the system is decaying to the fixed point with damped oscillation as the real part of the eigenvalue of the Jacobian is negative and the imaginary part is non-zero, but the noise keeps kicking the system out of the fixed point. Hence the system appears to follow a noisy oscillation.

We can say more quantitatively about the frequency distribution of this quasi-cycle. The SDEs (11.15) and (11.16) can be expressed as Langevin equations

$$\frac{dX}{dt} = J_{11}X + J_{12}Y + \sum_{k=1}^4 \tilde{b}_{1k}R_k(t), \quad (11.20)$$

$$\frac{dY}{dt} = J_{21}X + J_{22}Y + \sum_{k=1}^4 \tilde{b}_{2k}R_k(t), \quad (11.21)$$

with J defined as Jacobian (11.18) and

$$\langle R_i(t) \rangle = 0, \langle R_i(t)R_j(t') \rangle = 0 \quad \text{for } i \neq j, \quad (11.22)$$

$$\langle R_i(t)R_i(t') \rangle = \delta(t - t'). \quad (11.23)$$

It is easy to calculate the power spectrum density $P_X(\omega)$ and $P_Y(\omega)$ from (11.20) and (11.21), which corresponds to the Fourier transform of the auto-correlation in the steady state fluctuation (Wiener-Khintin theorem). Hence, the peak of the power spectrum density will tell us the frequency distribution of the quasi-oscillation. Here, the power spectrum density is defined as before, by using

$$\tilde{X}(\omega) = \int_{-\infty}^{\infty} X(t)e^{i\omega t}dt, \quad \tilde{Y}(\omega) = \int_{-\infty}^{\infty} Y(t)e^{i\omega t}dt \quad (11.24)$$

as

$$2\pi\delta(\omega - \omega')P_X(\omega) = \langle \tilde{X}(\omega)\tilde{X}^*(\omega') \rangle, \quad 2\pi\delta(\omega - \omega')P_Y(\omega) = \langle \tilde{Y}(\omega)\tilde{Y}^*(\omega') \rangle. \quad (11.25)$$

Using the Fourier-transformed Langevin equations

$$-i\omega\tilde{X}(\omega) = J_{11}\tilde{X}(\omega) + J_{12}\tilde{Y}(\omega) + \sum_{k=1}^4 \tilde{b}_{1k}\tilde{R}_k(\omega), \quad (11.26)$$

$$-i\omega\tilde{Y}(\omega) = J_{21}\tilde{X}(\omega) + J_{22}\tilde{Y}(\omega) + \sum_{k=1}^4 \tilde{b}_{2k}\tilde{R}_k(\omega), \quad (11.27)$$

(here $\tilde{R}_i(\omega) = \int_{-\infty}^{\infty} R_i(t)e^{i\omega t}dt$), it is straightforward to show (advanced exercise)

$$P_X(\omega) = \frac{J_{12}^2 \sum_{k=1}^4 \tilde{b}_{1k}^2 - 2J_{12}J_{22} \sum_{k=1}^4 \tilde{b}_{1k}\tilde{b}_{2k} + (J_{22}^2 + \omega^2) \sum_{k=1}^4 \tilde{b}_{2k}^2}{(J_{21}J_{12} - J_{11}J_{22} + \omega^2)^2 + (J_{11} + J_{22})^2\omega^2}, \quad (11.28)$$

$$P_Y(\omega) = \frac{J_{21}^2 \sum_{k=1}^4 \tilde{b}_{2k}^2 - 2J_{21}J_{11} \sum_{k=1}^4 \tilde{b}_{2k}\tilde{b}_{1k} + (J_{11}^2 + \omega^2) \sum_{k=1}^4 \tilde{b}_{1k}^2}{(J_{21}J_{12} - J_{11}J_{22} + \omega^2)^2 + (J_{11} + J_{22})^2\omega^2}. \quad (11.29)$$

If you plot these power spectrum densities, it has a peak at a finite frequency, indicating that the fluctuation contains periodic oscillatory components.

In Fig. 11.3, the simulated trajectories and the power spectrum densities are shown. The theoretical prediction (11.28)-(11.29) agrees well with the data. The peak matches the frequency expected from the eigenvalues.

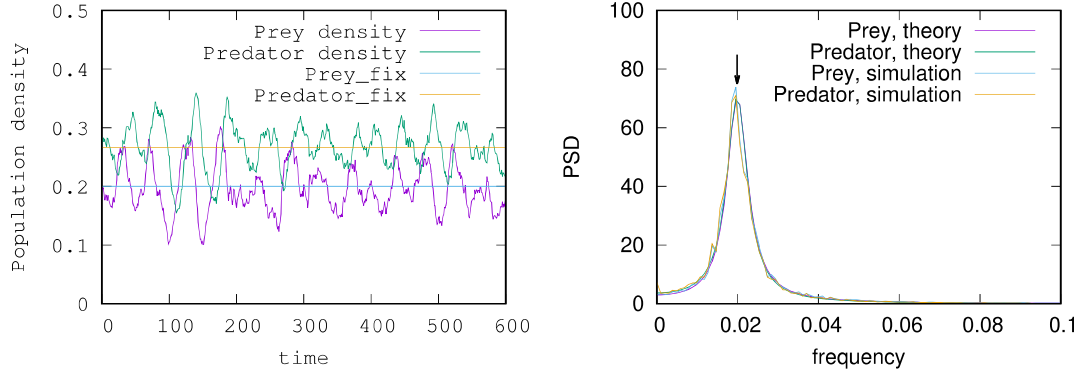


Figure 11.3: Left: An example trajectory obtained by Gillespie simulation. Plotted quantities are Density N/K and M/K . The horizontal lines show the coexistence fixed-point. Right: Comparison between the theoretically obtained power spectrum densities (11.28)-(11.29) and numerically calculated power spectrum density from Gillespie simulation (power spectrum densities were calculated from independent 64 simulations for time duration 2^{10} with initial condition close to the coexistence fixed point and averaged over the samples.). The arrow indicates the frequency expected from the complex part of the eigenvalue of Jacobian, $\frac{\alpha\delta}{2\gamma} \sqrt{-1 + 4\frac{\gamma^2}{\alpha\delta} \left(1 - \frac{\delta}{\gamma}\right)} / 2\pi$. Parameters used are $K = 1000$, $\alpha = 0.2$, $\beta = 0.1$, $\gamma = 0.5$, $\delta = 0.1$.

11.4 Summary

- Predator-Prey system was analyzed as an example of a 2-variable stochastic system.
- Even if the deterministic equation gives a stable fixed point with damped oscillation, the noise can induce "quasi-oscillation".
- Using the expansion of the master equations and SDEs, it is possible to calculate power spectrum density. The calculated power spectrum density gives a peak at a specific frequency, consistent with the quasi-oscillation seen in the simulation.

11.5 Exercise

1. Show that the SDEs (11.10) and (11.11) gives the Fokker-Planck equation (11.9).
2. * Simulating predator-prey model.
 - (a) Perform Gillespie simulation of the agent-based predator-prey model defined in section 11.1. Use the following parameters: $K = 1000$, $\alpha = 0.2$, $\beta = 0.1$, $\gamma = 0.5$, and $\delta = 0.1$. Plot the time course of the population densities N/K and M/K . Compare it with what is expected from the mean-field model's fixed points.
 - (b) If the initial condition is not too close to zero for both of the populations, the behaviour should look like noisy oscillation around the coexistence fixed point. Is the period of this quasi-oscillation consistent with what you expect from the eigenvalues 11.19? Calculate the expected typical period from eq. (11.19).
 - (c) Plot the theoretically evaluated power spectrum (11.28) and (11.29) as a function of the angular frequency ω . Does the peak correspond to the typical oscillation period you see?

Advanced exercise

3. Derive SDEs (11.15) and (11.16) by substituting eqs. (11.13) and (11.14) into eqs. (11.10) and (11.11) and collecting the highest order of K (which will be \sqrt{K}).

4. Derive the power spectrum densities (11.28) and (11.29) from (11.26) and (11.27).
5. * Numerically integrate the SDEs for the noise term (11.15) and (11.16) and plot the time course. Does it look similar to what you got in the Gillespie simulation? Tips: When you compare, pay attention to the correspondence between (N, M) and (X, Y) .
6. * Numerically calculate the power spectrum density of the Gillespie simulation and confirm that it agrees with the theory. Note: It may take some time to collect enough data. Also, there are some tools to do power spectrum density calculation but they may have different normalizations.

11.6 Further reading

This chapter is based on [24, 9]