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Summer term 2021

Biological Physics II

Problem Set 1

Solutions were to be handed in before 12:00 noon on Wedenesday, April 21, 2021.

1. Classical mechanics

1+4+3 = 8 points

Consider a particle with position x and momentum p, and obeying a Hamiltonian

$$H = \frac{p^2}{2} + U(x).$$

a) Write down the equations of motion of this system as two coupled first-order differential equations. Do you expect this system to exhibit a stable fixed point? Explain qualitatively.

Solution: $\dot{x} = p,\ \dot{p} = -\frac{dU}{dx}$. The system cannot have a stable fixed point. This can be argued as follows. A fixed point must have the coordinate $p = 0$. If the fixed point is stable, any point in phase space displaced from the fixed point along the p-axis by a sufficiently small amount must relax to the fixed point; but this would violate energy conservation.

Note: This question, as well as parts b) and c), intended to ask about attracting or asymptotically stable fixed points. A common definition of "stable" also includes fixed points that have trajectories that remain arbitrarily close to it. In this sense, the system can indeed contain stable (but not attracting) fixed points, namely any local minimum of the potential $U(x)$ together with $p = 0$.

b) Consider the potential $U(x) = -\frac{1}{2}x^2 + \frac{1}{4}x^4$. Numerically simulate $x(t)$ and $p(t)$ with the initial condition $x(0) = 0$, $p(0) = 1$, over the time interval $t = 0$ to $t = 15$. Plot $x(t)$ and $p(t)$. Do you observe a fixed point in the results? Plot the orbit of the system in the $x - p$ plane. Derive an exact expression for the curve you obtain. (Hint: Energy conservation.)

Solution: See Fig 1 for the numerical plots. Energy is conserved, and therefore the system must obey $\frac{1}{2}p(t)^2 - \frac{1}{2}x(t)^2 + \frac{1}{4}x(t)^4 = E(0)$, where the initial energy $E(0) = \frac{1}{2}p(0)^2 - \frac{1}{2}x(0)^2 + \frac{1}{4}x(0)^4 = \frac{1}{2}$. Therefore the curve in the $x - p$ plane is $p^2 - x^2 + \frac{1}{2}x^4 = 1$.

c) Now add a friction force term $-p$ to the equation of motion, and repeat the numerical exercise in the previous part. Explain in words why you see a fixed point in this case.

Solution: The equation for the momentum is modified to $\dot{p} = -\frac{dU}{dx} - p$. See Fig 1. The potential minima are at $x = \pm 1$, and the fixed points $x = 1, p = 0$ and $x = -1, p = 0$ are now attracting fixed points. The initial condition in this case belongs to the basin of attraction of $x = 1, p = 0$. The friction term dissipates energy till the particle comes to rest at the local minimum at $x = 1$.

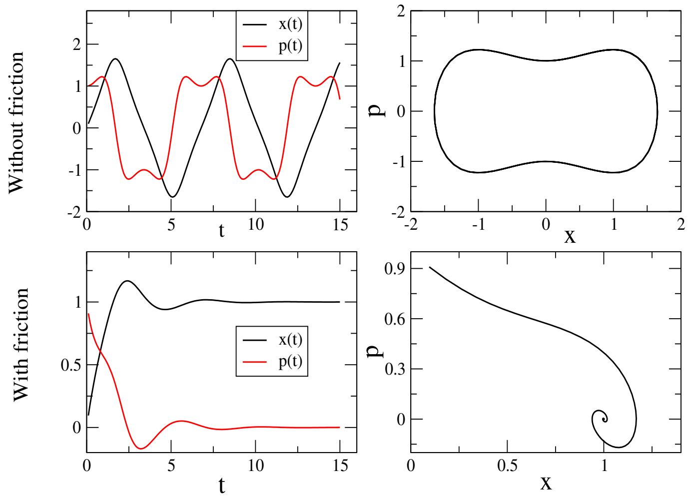

Figure 1: Plots for problem 1.

2. Insect population dynamics

3+2+5+6+3+3=22 points

An insect population has size N, the evolution of which is governed by the equation

$$\frac{dN}{dt} = RN\big(1 - \frac{N}{K}\big) - p(N). \tag{2.1}$$

The first term is a logistic growth term, where R is the population growth rate at small population size, and K is the carrying capacity of the environment. The second term $p(N)$ is the population decrease rate due to predation, and is given by

$$p(N) = \frac{BN^2}{A^2 + N^2}. \tag{2.2}$$

All parameters are assumed to be positive.

a) By an appropriate transformation, the equation (2.1) can be written in terms of dimensionless variables x, τ and dimensionless parameters r, k as

$$\frac{dx}{d\tau} = rx\big(1 - \frac{x}{k}\big) - \frac{x^2}{1 + x^2}. \tag{2.3}$$

Find the transformation between the original variables and parameters in equation (2.1) and those in (2.3).

Solution: The transformation is

$$x = \frac{N}{A},\ \tau = \frac{BT}{A},\ r = \frac{RA}{B},\ k = \frac{K}{A}.$$

b) We now focus on analyzing (2.3). Show that this equation has a fixed point $x^* = 0$ for all parameter values. We call this the trivial fixed point. Prove that it is unstable. Show analytically that for fixed r and sufficiently small k, the system has only one non-trivial fixed point. Is it stable or unstable?

Solution: The fixed point equation is

$$rx\big(1 - \frac{x}{k}\big) = \frac{x^2}{1 + x^2}$$

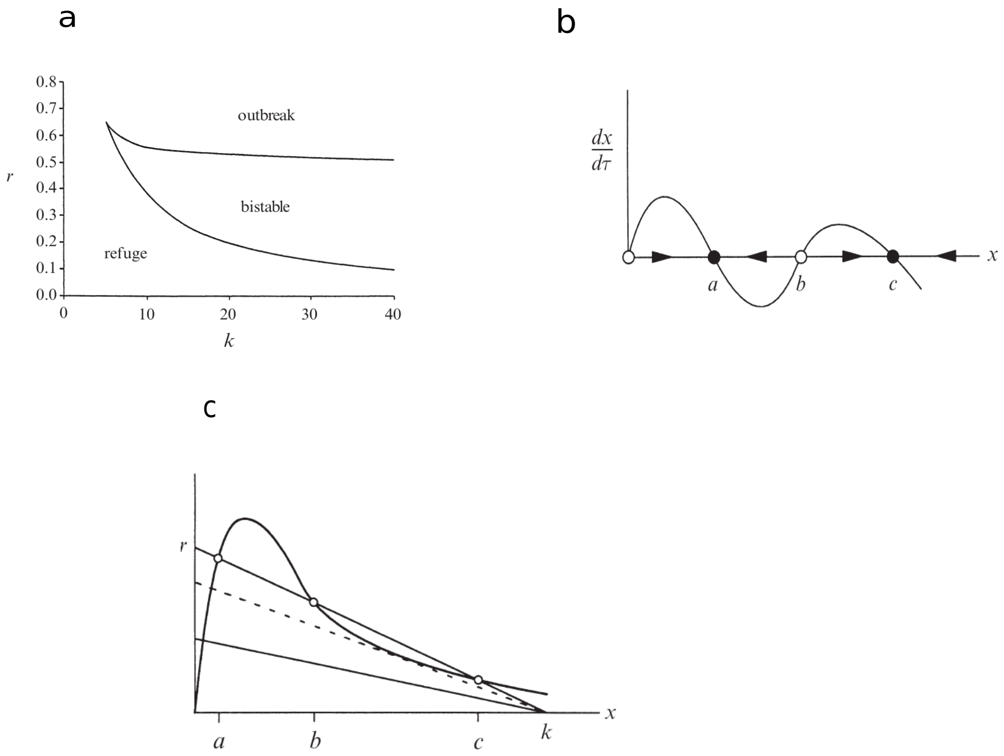

Figure 2: Figure adapted from *Nonlinear dynamics and chaos, Steven H. Strogatz, 2018.*

and $x = 0$ clearly satisfies the equation. Linearizing (2.3) at $x = 0$ gives $\frac{dx}{d\tau} \approx rx$, showing that x is unstable since $r > 0$. The non-trivial fixed points are the positive zeroes of the function

$$F(x) = g_1(x) - g_2(x),$$

where $g_1(x) = r(1 - x/k),\ g_2(x) = x/(1 + x^2)$. Notice that $F(0) = r > 0$ and $F(\infty) < 0$, and thus there must be at least one zero of this equation. The derivative of the function is

$$F'(x) = -\frac{r}{k} - \frac{1 - x^2}{(1 + x^2)^2}.$$

Since the second term is bounded, a sufficiently small k will ensure that the first term dominates, making $F'(x) < 0$ for all x, which implies that $F(x)$ is monotonic decreasing and therefore has exactly one zero. The corresponding fixed point must be stable since the trivial fixed point is unstable.

c) As k is increased, the number of non-trivial fixed points changes through bifurcations. To understand the bifurcation structure of the full model, prove that at a bifurcation point, r and k must have the parametric form

$$r = \frac{2y^3}{(1 + y^2)^2};\ k = \frac{2y^3}{y^2 - 1}. \tag{2.4}$$

Solution: At a bifurcation point, a fixed point y must satisfy the equations $g_1(y) = g_2(y)$, $g_1'(y) = g_2'(y)$. These two equations lead to (2.4) after a few steps of algebra.

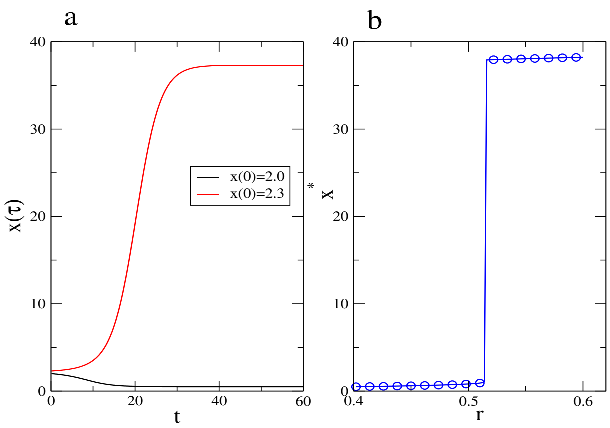

Figure 3: **a**. Solution to part (e). **b**. Solution to part (f).

d) Numerically plot the curve generated by (2.4) in the $r-k$ plane. You should find that the curve separates the plane into three regions. What is the number of non-trivial fixed points in each of these regions, and what are their stabilities? Explain how you obtain your answers. For the region with three non-trivial fixed points, sketch the flow diagram on the x-axis. (Notice that two of these three non-trivial fixed points are stable; the smaller value is called the *refuge* level of the insect population, while the larger value is called the *outbreak* level.)

Solution: See Fig 2a for the three regions. The region labelled *refuge* has one non-trivial fixed point (stable), namely the one mentioned in the previous part. The region *outbreak* also has one fixed point (stable). The region *bistable* has the coexistence of two stable fixed points (point a, the refuge level; point c, the outbreak label) separated by an unstable fixed point (at b). See Fig 2b for the flow diagram in the bistable region.

The fixed points can be analysed by the figure 2c, which shows the functions $g_1(x)$ (straight lines) and $g_2(x)$ (curved line). The intersections of the two functions give the fixed points. The intersections on the lower straight line belong to the refuge region, and those on the upper straight line belong to the bistable region. The outbreak region corresponds to an even higher straight line obtained for larger r (not shown). The stabilities can be obtained from the fact that for flows on the line, stable and unstable fixed points must alternate (except exactly at bifurcation points, where a fixed point may attract points from one side but repel points on the other).

e) Consider the case $r = 0.4$, $k = 40$, which belongs to the region with three non-trivial fixed points. Numerically simulate $x(\tau)$ with the two different initial conditions $x(0) = 2$ and $x(0) = 2.3$. In both cases, let the simulations run for enough time such that the system nearly reaches a fixed point. Plot both the trajectories in the same graph. Estimate the refuge and outbreak levels in this system from the plots.

Solution: See Fig 3a for the numerical plots. The refuge level corresponds to the initial condition $x = 2.0$, and is approximately 0.491, whereas the outbreak level corresponds to the initial condition 2.3, and is approximately 37.3.

f) Consider a small variation of the problem, where the parameter r is allowed to change slowly in time. Assume that the change is quasistatic, i.e the population is always at a fixed point of (2.3) at any value of r. Starting with the parameters $r = 0.4$, $k = 40$ and the population at the refuge level for these parameters, implement an algorithm to increase r quasistatically up to 0.6. Plot x as a function of r. Find the value of r at which the population jumps from the refuge level to the outbreak level. Explain the jump in terms of bifurcations.

Solution: See Fig 3b for the numerical plot. We start the numerics in the bistable region and at the refuge level, but as r increases to (approximately) 0.513, a bifurcation occurs, moving the model parameters to the outbreak region where the refuge level is unstable, leaving the outbreak level as the only stable fixed point. As a result, the system jumps to the outbreak level.

Note: Many aspects of problem 2 are discussed in detail in Section 3.7 of *Nonlinear dynamics and chaos with student solutions manual: With applications to physics, biology, chemistry, and engineering, Steven H. Strogatz, CRC press, 2018.*