

STUDENT VERSION

Do Runners Synchronize?

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STATEMENT

Oscillatory systems exist throughout the natural world. Prominent examples of oscillators include the position of a mass in a frictionless mass-spring system, the position of a swinging pendulum, the number of daylight hours over a year, predator-prey population sizes, electrical activity in brain cells, and light flashes in fireflies. Perhaps the most famous example of oscillatory behavior in ecology comes from data collected by The Hudson's Bay Company on the snowshoe hare and the Canadian lynx. Several different systems of differential equations have been developed to describe these populations. One such system is the Ronsenzweig-MacArthur model, which consists of two differential equations and which under certain parameter values yields the results shown in Figure 1.

A striking phenomenon that has been observed in many of the above systems is that in the presence of a second nearby oscillator, the two will often synchronize. This was first observed by Christiaan Huygens in the 17th century, where pendulum clocks resting on the same support beam will eventually synchronize. Since then, synchrony has been observed in the flashing of fireflies, in spatially distinct predator-prey populations, and in coupled brain cells. In this modeling scenario we will find and classify the equilibria of a differential equation that determines whether or not two oscillators will synchronize.

Let us start by describing a single predator-prey oscillator. The left panel of Figure 1 shows prey and predator populations as a function of time and shows periodic behavior with a period of $T = 19.06$ time units. This means that for any given time t the prey populations is the same at time t and at time $t + 19.06$, likewise for the predator. The right panel of Figure 1 is the phase plane and displays the prey and predator populations relative to each other. As time is increased,

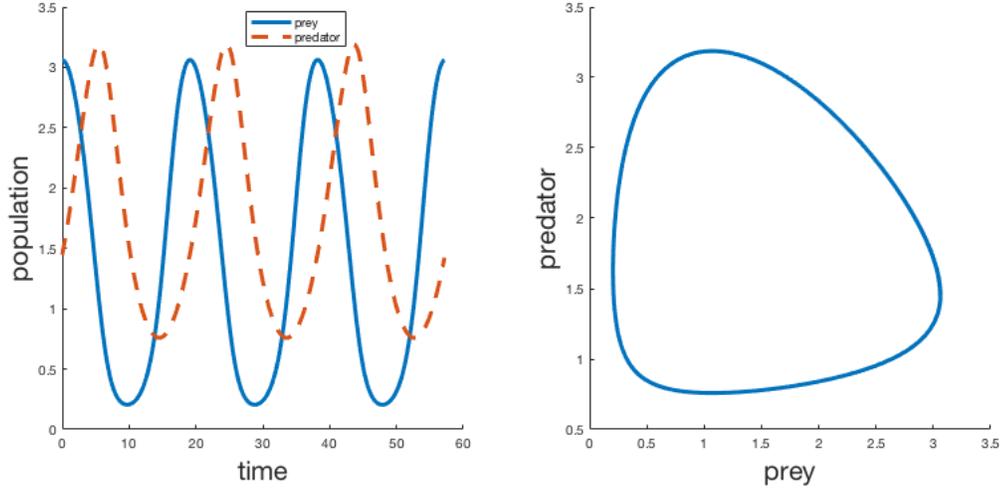


Figure 1. Simulation of the Rosenzweig-MacArthur predator-prey model. The left panel displays the time-series of the prey and predator populations while the right panel displays the limit cycle in the phase plane. The populations move counterclockwise around the closed loop on the right panel as time increases. This figure displays three oscillations, but these oscillations continue indefinitely.

the system moves counterclockwise and completes a cycle every T time units. This model consists of two differential equations, one describing the prey population and one describing the predator population. However, because the system has periodic behavior, we don't have to keep track of both the prey and predator populations individually. We can instead study the system by introducing a new variable called the *phase*, θ , which measures how far around the cycle the system is. This one variable describing the phase gives the same information as the two variables describing the prey and the predator. We can now describe our system with one differential equation instead of two! Since the system has period T , the phase must also have period T , i.e. $\theta \in [0, T)$, with $\theta(0) = \theta(T)$.

Before we study our predator-prey system further, we start with a simpler system. Our new system also has two differential equations, but instead of the oddly shaped orbit seen in the right side Figure 1, our new system moves counterclockwise around the unit circle at a constant velocity of 1 radian per time unit (right panel Figure 2). From the left panel of Figure 2, we can see that both $x(t)$ and $y(t)$ are periodic functions with period 2π , i.e. $x(t) = x(t) + 2\pi$. Because $T = 2\pi$, we say that x , y , and θ are defined on the circle.

Since we stated above that the system has a constant velocity of 1 radian per time unit, θ is described by the following differential equation:

$$\frac{d\theta}{dt} = 1 \tag{1}$$

To better visualize this system, let's think of θ as the position of a runner on this unit-circle track, with the differential equation $\frac{d\theta}{dt}$ describing the velocity of the runner. The left panel of Figure

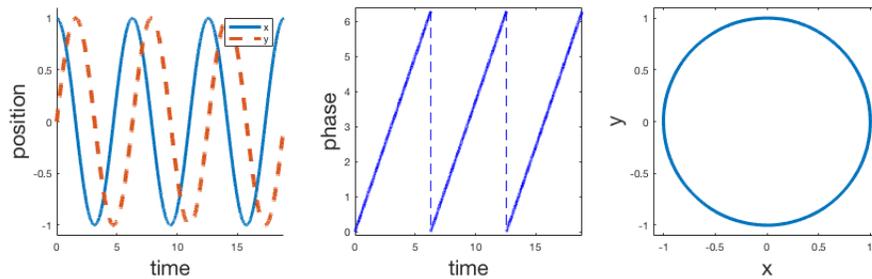


Figure 2. Simulation of an oscillator that moves around the circle counterclockwise with a velocity of 1 radian per time unit. The left panel displays the time-series of the x and y coordinates. The middle panel displays the phase. The right panel displays the limit cycle in the phase plane. This figure displays three oscillations, but these oscillations continue indefinitely.

2 show the x - and y -coordinates as a function of time, the middle panel shows the phase, $\theta(t)$. Let $\theta = 0$ refer to the right side of the track where $x = 1$ and $y = 0$. Notice that while (1) would seem to indicate that θ increases monotonically, because it exists on the circle its domain is restricted to $[0, 2\pi)$, with $\theta(0) = \theta(2\pi)$ as can be seen in the middle panel of Figure 2.

1. Assume that the runner has constant velocity measured in radians per hour. Write the differential equation $\frac{d\theta}{dt}$ that satisfies each of the following:
 - (a) The runner maintains a constant velocity of ω .
 - (b) The period of the runner (length of time it takes for the runner to complete one lap) is 1 hour.
 - (c) The period of the runner is 10 hours.

Now let us add a second runner to this unit circle track and explore what happens if the two runners are attracted to each other, i.e. if a runner is behind the other runner she will speed up and if she is ahead of the other runner she will slow down. For now let us assume that the two runners are identical in their individual velocity, ω , and in how their velocity changes due to the presence of another runner. In the context of our predator-prey model, the two runners could represent the populations in the phase plane of animals in two separate habitats and the change in runner velocity could take the form of animals migrating between from the

more dense habitat to the less dense one. If we assume that the runners attraction to each other is the sine of their difference in phase, then the velocities of the two runners can now be described by the following system of two differential equations (this formulation is known as the Kuramoto Model):

$$\begin{aligned}\frac{d\theta_1}{dt} &= \omega + \frac{a}{2} \sin(\theta_2 - \theta_1) \\ \frac{d\theta_2}{dt} &= \omega + \frac{a}{2} \sin(\theta_1 - \theta_2)\end{aligned}\tag{2}$$

The parameter a describes how much a runner slows down or speeds up due to the presence of the other runner.

2. For each scenario below sketch the position of the two runners on the unit circle and calculate their velocities. Let $\omega = 3$ and $a = 1$.
 - (a) Runner 1 is at $\theta_1 = \frac{\pi}{6}$ and runner 2 is at $\theta_2 = 0$
 - (b) Runner 1 is at $\theta_1 = \frac{\pi}{3}$ and runner 2 is at $\theta_2 = \frac{\pi}{6}$
 - (c) Runner 1 is at $\theta_1 = \frac{\pi}{2}$ and runner 2 is at $\theta_2 = 0$
 - (d) Runner 1 is at $\theta_1 = 0$ and runner 2 is at $\theta_2 = \frac{\pi}{2}$
 - (e) Runner 1 is at $\theta_1 = 0$ and runner 2 is at $\theta_2 = \pi$

3. What values of a would correspond to the opposite situation, where the runners are repelled by each other? We see this phenomenon in inhibitory neurons, whose action potentials inhibits other nearby neurons from having an action potential.

It is often the case in these types of systems that we would not care about the phase of each individual oscillator (the position of each runner), only about the difference between the two phases (distance between the two runners). Let's define the *phase difference*, $\phi(t) \in [0, 2\pi)$, as:

$$\phi = \theta_1 - \theta_2\tag{3}$$

4. Phase difference:
 - (a) If $\phi = 0$, what does that say about the two runners?
 - (b) If $\phi = \pi$, what does that say about the two runners?

- (c) If $\phi = 2\pi$, what does that say about the two runners?
 - (d) If $\phi = \pi/2$, what does that say about the two runners?
 - (e) If $\phi = 3\pi/2$, what does that say about the two runners?
 - (f) Sometimes ϕ is defined as $\phi \in [-\pi, \pi)$. Why is this sometimes considered more intuitive?
5. Find $\frac{d\phi}{dt}$. First take the derivative of both sides of (3), then substitute using (2), and then simplify. (Hint: sine is an odd function)
6. Find all equilibria for the phase difference.
7. Classifying the equilibria.
- (a) Sketch a graph with $\frac{d\phi}{dt}$ on the vertical axis and ϕ on the horizontal axis. Use this graph to classify the stability of all equilibria.
 - (b) Let $G(\phi) = \frac{d\phi}{dt}$. Classify each equilibria by finding $G'(\phi)$ and evaluating it at each equilibria.
 - (c) What would change in (a) and (b) if we let $a < 0$?
8. Based on our equilibria calculations above, what do we expect to happen to the runners if we let them run for a long time? Assume they are in excellent physical shape and never get tired.
9. Let's find an expression for ϕ based on the differential equation you found in Question 5 to see if it agrees with your above equilibria analysis.
- (a) Use the method of separation of variables to integrate the differential equation you found in Question 5. Solving for ϕ explicitly requires some tricky trigonometric identities so it may be easier to leave as an implicit expression.
 - (b) Use a graphing utility to graph your solution to (a). If necessary, make sure the graphing utility can handle implicit expression (such as desmos.com).
 - (c) Does this graphical solution agree with the equilibria you found?

What if the runners no longer have the same independent velocities? We can model this by adding the terms ω_1 and ω_2 to (2) such that $\omega_1 \neq \omega_2$:

$$\begin{aligned}\frac{d\theta_1}{dt} &= \omega_1 + \frac{a}{2} \sin(\theta_2 - \theta_1) \\ \frac{d\theta_2}{dt} &= \omega_2 + \frac{a}{2} \sin(\theta_1 - \theta_2)\end{aligned}\tag{4}$$

10. Let runner 1 be slightly faster than runner 2:

$$\omega_1 - \omega_2 = 1/3$$

Let $a = 1$.

- Find $\frac{d\phi}{dt}$.
- Find and classify all equilibria (sketch $\frac{d\phi}{dt}$ on the vertical axis and ϕ on the horizontal axis).
- What do we expect to happen to the runners if we let them run for a long time (assume they are in excellent physical shape and never get tired).

11. Consider the situation where runner 1 is much faster than runner 2:

$$\omega_1 - \omega_2 = 2$$

Let $a = 1$.

- Find $\frac{d\phi}{dt}$.
- Find and classify all equilibria.
- What do we expect to happen to the runners if we let them run for a long time (assume they are in excellent physical shape and never get tired)

12. Bifurcation

- Considering Questions 10 and 11, what can we say about the relationship between $\omega_1 - \omega_2$ and a that is required for equilibria to exist?
- Describe how the equilibria change as the difference in speeds is increased from 0 to 2.

Let us return to our predator-prey system of Figure 1. Assume that coupling between the oscillators takes the form of migration and that prey and predators leave the higher population oscillator and move to the lower population oscillator.

13. If we reduce the predator-prey to a phase model, what can we say about the value of a ?

In our previous phase model (4), the change in a runner's speed due to the other runner was only a function of the difference in phases between the two runners. In other words, if runner 1 was 1/4 lap behind runner 2, she would speed up the same amount regardless of where on the track they both were. This is not going to be true in our predator-prey model because the movement around the cycle (track) is not constant, see the right panel of Figure 1. Therefore, the effect of migration on the oscillator depends on the phase difference between the oscillators and also on the phase of that oscillator. Additionally, we want to allow for a different coupling function as it is unlikely that animal migration should follow a sine curve. Now the differential equations describing the phase of each oscillator (4) are written:

$$\begin{aligned}\frac{d\theta_1}{dt} &= \omega_1 + \frac{a}{2}h_1(\theta_2 - \theta_1) \\ \frac{d\theta_2}{dt} &= \omega_2 + \frac{a}{2}h_2(\theta_1 - \theta_2)\end{aligned}$$

The effect of migration on the velocity around the cycle of the predator-prey populations in patch 1 and 2 is described by the functions h_1 and h_2 , respectively. To reduce the original predator-prey system to this phase model requires that migration be small compared to the predation, reproduction, and death rates of the populations. Actually calculating or approximating the functions h_1 and h_2 requires asymptotic analysis or perturbation theory and it is beyond the scope of a first differential equations course. However, we will skip the details of the mathematical derivation and as in Question #10, we can find a differential equation describing the difference in phase between the two oscillators using the above phase model and 3. Letting $\omega = \omega_1 - \omega_2$ and $H(\phi) = \frac{a}{2}(h_1(-\phi) - h_2(\phi))$, we get:

$$\frac{d\phi}{dt} = \omega + H(\phi)$$

The function $H(\phi)$ is often called the interaction function and depending on its properties, the above differential equations describing the change in phase difference can exhibit a variety of behaviors. Recall that because $\phi = 0$ is identical to $\phi = 2\pi$, we have previously found $\frac{d\phi}{dt}$ that lead to two different equilibria (Questions 6 and 10) and to no equilibria (Question 11).

14. Assume that the two predator-prey systems are identical, i.e. $\omega_1 = \omega_2$ and $h_1 = h_2$. Sketch a graph of $G(\phi) = \frac{d\phi}{dt}$ that leads to three or more equilibrium on the interval $[0, 2\pi)$. Describe the behavior of this equilibria behavior of this system and how it depends on initial conditions. Note that $G(\phi)$ and $H(\phi)$ are periodic functions with period 2π .

15. Assume $\omega_1 > \omega_2$ and $H(\phi)$ as in Question 14. Sketch several graphs of $G(\phi)$ as the difference between ω_1 and ω_2 increases. Describe what happens to the equilibrium.
16. Assume $\omega_1 \neq \omega_2$ and $h_1 \neq h_2$. Sketch a graph of $G(\phi)$ and find all equilibrium.