

Math Circle for October 30, 2002

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Extinction & Population Dynamics

When Europeans first arrived in the Americas, Passenger Pigeons were perhaps the most populous bird in the area. At that time, the size of the Passenger Pigeon population was somewhere between 3 to 5 billion. Residents of the Eastern United States wrote that “There are wild pigeons in winter beyond number or imagination. . . . I myself have seen three or four hours together flocks in the air, so thick that even have they shadowed the sky from us.” Despite the enormous number of birds present in the United States in the 1700’s, there are no Passenger Pigeons left on earth today, as the last known bird (Martha) died in captivity in 1914. The Passenger Pigeon was hunted and killed by humans for many years before its extinction. During this time, the number of pigeons in the United States decreased, but no one seemed to expect the birds to disappear completely. Could scientists have predicted the extinction of the Passenger Pigeon using mathematics? We’ll start to answer this question by looking at some mathematical models of fish ponds.

POND 1

First, consider a pond that is inhabited by one type of fish. What factors determine how many fish are in the pond from one day (month, year) to the next? In real life, the number of fish in the pond at some later time probably depends on a variety of factors including the number of fish currently in the pond, the amount of food available to the fish, the number of predators that eat the fish, and the environmental conditions of the area around the pond (temperature, pollution levels). Instead of thinking of the exact number of fish in the pond, we can also consider how full the pond is. Assume that the fraction of the pond that is full of fish one month from now (represented by N_1) depends on how full the pond currently is (N_0) and the following equation:

$$N_1 = \frac{2N_0}{1 + 2N_0}$$

Remember that we are thinking of only how full the pond is, or alternatively

of the fraction of the pond that contains fish. Therefore, N_0 and N_1 must be between 0 and 1. A more general form for this equation is:

$$N_{t+1} = \frac{2N_t}{1 + 2N_t}$$

where N_t is the fraction of the pond that is full of fish during month t , and N_{t+1} is the fraction of the pond that is full of fish during month $t + 1$.

What does this function look like and how can we use it to determine how full the pond will be at some time in the future? To get an idea of what this function actually tells us, let's look at a few specific examples. Assuming that the pond starts out with N_0 fish, how full will it be one month from now?

Exercise 1a: Find N_1 when:

$$N_0 = 0 \quad N_1 = 0$$

$$N_0 = \frac{1}{4} \quad N_1 = \frac{1}{3}$$

$$N_0 = \frac{1}{2} \quad N_1 = \frac{1}{2}$$

$$N_0 = \frac{3}{4} \quad N_1 = \frac{3}{5}$$

$$N_0 = 1 \quad N_1 = \frac{2}{3}$$

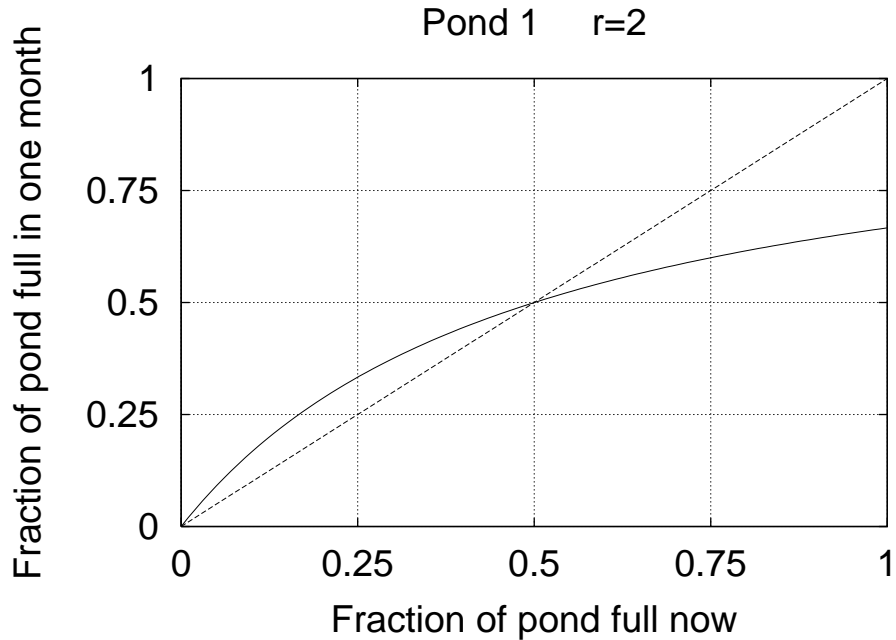
Now, plot these points on a graph to get an idea of what the function looks like.

Exercise 1b: How full will the pond be after ten years if it starts out one quarter full? One way to figure this out is to calculate the function over and over again. Writing out the first numbers in this sequence we find:

$$N_0 = \frac{1}{4} \quad N_1 = \frac{1}{3} \quad N_2 = \frac{2}{5} \quad N_3 = \frac{4}{9} \quad N_4 = \frac{8}{17} \quad N_5 = \frac{16}{33}$$

It looks like the numbers are getting closer and closer to $\frac{1}{2}$. In fact, if we complete the calculations we find that the pond will be half full in ten years. What if we want to determine how full the pond will be fifty years from now? This gets to be pretty hard to calculate, so it would be nice to have a faster way to figure this out.

COBWEBBING



The first method we will talk about is a graphical method called cobwebbing. Let's assume that the pond starts out a quarter full. We have already figured out that one month from now, the pond will be one third full. Looking at the graph that we've drawn of the function, we see that if we draw a vertical line starting at $\frac{1}{4}$ on the x-axis, and stop when we hit the population curve, we will be at a height of $\frac{1}{3}$. For the next iteration, we want to start at $\frac{1}{3}$ on the x-axis. We can make this easy by drawing a second line on the graph corresponding to the function $y = x$ or $N_1 = N_0$. Now, starting at the height of $\frac{1}{3}$ we draw a horizontal line until we intersect the line $y = x$. This point will correspond to a value of $\frac{1}{3}$ on the x-axis, or $N_0 = \frac{1}{3}$. Now, draw a vertical line from this point until we intersect the population curve again. This will give us the next population size. We can continue this process indefinitely.

After about six iterations we notice something interesting. That is, we seem to be sitting on both the population curve and the line $y = x$ and not moving anywhere from one iteration to the next. For this particular population, the pond seems to become half full and then not change at all. In our initial calculations, we found that if the pond is half full at first, then after one month it is still half full. So, once the pond is half full, it will always be half

full no matter how long we observe the pond. We call the special population sizes where this occurs **equilibrium points**.

Are there any other equilibrium points for this system and how can we find them? From our earlier calculations we notice that if the pond is completely empty, it will always be empty from one month to the next, so zero is another equilibrium point. These points are easy to locate on the graph as they are the only two places where the population curve and the line $y = x$ intersect.

Exercise 1c: What happens for other initial population sizes? Try using the cobwebbing technique for $N_0 = \frac{3}{4}$ and $N_0 = 1$. In both cases we find that the pond is eventually half full, even though it started out with more fish than before.

What does this mean biologically? From our cobwebbing, it seems like no matter how full the pond is at first, as long as there are some fish in the pond to start, the pond will eventually be half full. If there are very few fish in the pond, there is plenty of food for all to eat, so the population grows. If there are too many fish in the pond, there is not enough food, so some of the fish die. In this case it looks like the perfect situation is for the pond to be half full of fish. We call the state of the pond being half full a **stable equilibrium**, since the pond always becomes half full, no matter how full it is to start. If the pond starts out with no fish in it, there is no way for fish to appear, so the pond remains empty. We call the state of the pond being empty an **unstable equilibrium** since the pond will only remain empty if it starts out being empty. If we add any fish, no matter how few, the pond will eventually become half full.

ALGEBRAIC TECHNIQUE

Can we prove using algebra that the equilibrium points we found using cobwebbing are in fact the only equilibrium points? We defined an equilibrium point to be an initial population size for which the population size remains constant from one month to the next. Mathematically this means that $N_1 = N_0$, or $N_{t+1} = N_t$ for all t . To figure out where this occurs we can solve the equation:

$$N = \frac{2N}{1 + 2N}$$

Multiplying, we get the polynomial $N(2N - 1) = 0$. So, the only possible values of N that work are $N = 0$ and $N = \frac{1}{2}$, which are the exact values we found graphically.

GENERAL r

So far, we have looked at a very specific equation. Let's assume now that the population size is determined by the equation:

$$N_1 = \frac{rN_0}{1 + 2N_0}$$

where r is the distance of the pond from a big city, say Salt Lake. How does r affect how full the pond is after a long time?

Exercise 2a: Using cobwebbing, predict how full the pond will be after ten years if:

$$r = \frac{3}{4}, \frac{3}{2}, 3 \text{ and } N_0 = 0, \frac{1}{4}, \frac{1}{2}, \frac{3}{4}, 1$$

Exercise 2b: For the given values of r , use algebra to find the equilibrium points.

$$r = \frac{3}{4} \text{ has equilibrium points } N^* = 0 \text{ and } N^* = -\frac{1}{8}$$

$$r = \frac{3}{2} \text{ has equilibrium points } N^* = 0 \text{ and } N^* = \frac{1}{4}$$

$$r = 3 \text{ has equilibrium points } N^* = 0 \text{ and } N^* = 1$$

What does it mean to get a negative number?

Exercise 2c: Using algebra, figure out a rule for determining how full the pond will be after a long time for any value of r . When is there only one equilibrium point, and when are there multiple equilibrium points?

$$\text{Solve the equation } N = \frac{rN}{1+2N}$$

$$N + 2N^2 = rN$$

$$2N^2 + (1 - r)N = 0$$

$$N(2N + 1 - r) = 0$$

$$N = 0 \text{ and } N = \frac{r - 1}{2}$$

There will only be two equilibrium points if $r > 1$.

Exercise 2d: Think about what changing the value of r means biologically. How do the different values of r affect how full the pond is?

****Exercise 2e:** Can you figure out an equation for general N_t in the case when $r=2$? First look at the sequence of numbers generated earlier when $N_0 = \frac{1}{4}$. Do you see a pattern here?

$$N_t = \frac{2^t N_0}{1 + 2(2^t - 1)N_0}$$

BIOLOGICAL MEANING

What does it mean for r to change? From the work we've done so far, it looks like the number of fish that can survive in the pond is very dependent on the value of r we use. Small values of r mean that very few or no fish survive, and bigger values of r mean that more fish can survive in the pond. It is possible that the closer a pond is to a big city, the more polluted it is. If this is the case, our results imply that ponds close to cities, or in polluted areas, will only have small numbers of fish, whereas ponds far away from cities are more likely to be full or nearly full of fish. In fact, no fish can survive in ponds that are too close to the city ($r < 1$).

POND 2

Now let's consider a pond where the fish population size from one month to the next is determined by the equation:

$$N_1 = \frac{rN_0^2}{1 + 4N_0^2}$$

Using the same techniques as before, determine what will happen to the pond after ten years if:

$$r = 3, 4, 5 \text{ and } N_0 = \frac{1}{8}, \frac{3}{4}$$

Exercise 3a: Using cobwebbing predict how full the pond will be after ten years for the given values of r and N_0 .

Exercise 3b: For the given values of r , use algebra to find the equilibrium points. Note: In some cases, it is possible to have more than 2 equilibrium points.

$r = 3$ has equilibrium point $N^* = 0$

$r = 4$ has equilibrium points $N^* = 0$ and $N^* = \frac{1}{2}$

$r = 5$ has equilibrium points $N^* = 0$, $N^* = \frac{1}{4}$ and $N^* = 1$

Exercise 3c: Using algebra, figure out a rule for determining how full the pond will be after a long time for any value of r . How many equilibrium points are there?

Solve the equation $N = \frac{rN^2}{1+4N^2}$

$$N + 4N^3 = rN^2$$

$$4N^3 - rN^2 - N = 0$$

$$N(4N^2 - rN - 1) = 0$$

$$N = 0 \quad \text{and} \quad N = \frac{r \pm \sqrt{r^2 - 16}}{8}$$

There is one equilibrium point if $r < 4$, two equilibrium points when $r = 4$ and three equilibrium points if $r > 4$.

****Exercise 3d:** Plot a graph of the equilibrium points for all values of r . This type of graph is called a **bifurcation diagram**.

Exercise 3e: Can you think of a biological scenario that can explain what you see happening? Think about what happens when you start with different population sizes and different values of r .

Exercise 3f: How does this relate to the story of the Passenger Pigeon that we talked about initially? What if r is inversely related to the hunting rate (i.e. large r implies low levels of hunting, and small r implies high levels of hunting)? If the model for Pond 2 also describes the Passenger Pigeon population, does the equilibrium population size drop gradually as hunting increases (r decreases), or is there a sudden drop when hunting increases past a critical point?

Challenge Problem: Determine the long term dynamics of a population that behaves according to the equation:

$$N_{t+1} = \frac{rN_t}{1 + 4N_t^2}$$

A. Plot this function (you can use your calculator) and use the cobwebbing technique with the following values of r and N_0 :

$$r = 2, 4, 5$$

$$N_0 = .1, .9$$

B. Use your calculator to produce a short sequence of numbers using the initial population sizes given above.

Do you see new patterns appearing in the cobwebbing picture and numerical sequence that did not occur in Ponds 1 and 2? What are some possible biological explanations for the patterns you see?

C. Algebraically solve for the equilibrium points for general values of r . How many equilibrium points are there?