LAB 1.5 Modeling the Extinction of the Passenger Pigeon

In Section 1.7 we studied the logistic population model with terms added to model various types of harvesting. We saw how persistent harvesting at too great a level could render a species extinct. On the other hand, if harvesting is stopped before extinction, the logistic model predicts that any population will rebound to its carrying capacity. In nature, exponential growth is observed in some populations, but others hover near extinction for many generations.

When Europeans arrived in North America, they were astonished by the great flocks of passenger pigeons. It is estimated that, in the 1700s, there were three to five billion of these birds and that one-half of all birds in North America were passenger pigeons. They tasted pretty good and were easy to hunt and trap. The hunting and trapping of passenger pigeons and, to a lesser extent, the clearing of forests for agriculture are blamed for their extinction. Harvesting of passenger pigeons in large numbers continued in the Midwest until the 1860s and 70s. By 1890 the bird was extremely rare in the wild, and by 1900 it is likely that no wild birds remained. The last passenger pigeon died in 1914 at the Cincinnati Zoo.*

*An excellent book on the passenger pigeon and an excellent example of careful, complete research is A. W. Schorger, *The Passenger Pigeon: Its Natural History and Extinction*, University of Oklahoma Press, Norman, 1955.

The disappearance of the passenger pigeons raises two questions: First, how could harvesting affect such a gigantic population even if it was done on a very large scale? Second, why didn't the population rebound when harvesting stopped?

To investigate these questions, we use a logistic model with constant harvesting

$$\frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - C.$$

See Example in §1.7 p.65

$\frac{dP}{dt}$; (-)

(+)

(-)

We make (extremely rough) estimates of the parameters based on historical information of passenger pigeon biology. Each pair of pigeons laid only one egg per year. Hence, the absolute largest that the growth-rate coefficient could be is $k = 0.5$, and this value does not consider the death rate. Since the lifespan even in captivity was around twenty years and since the hatching and survival rate of squabs (baby pigeons) could not have been 100%, we know that k must have been significantly less than 0.5. For the sake of argument, we take the generous estimate of $k = 0.25$.

The carrying capacity must have decreased as native forests (particularly beech) were cleared for agriculture. Even by the early 1800s passenger pigeons were on the decline in the Northeast. However, native forest remained in the Midwest and large flocks were still observed there in the mid- to late-1800s. Again, in order to work with specific numbers, we make the rough and somewhat arbitrary estimate of $N = 50{,}000{,}000$ as the carrying capacity.

Your report should consider the following questions:

1. What is the largest sustainable harvesting rate if $k = 0.25$ $= \frac{1}{4}$ and $N = 50{,}000{,}000$? (Note: This number comes out very high. Perhaps the most remarkable thing about passenger pigeons was their preference for large, tight flocks. When shot, the flock would quickly regroup even more tightly. While the passenger pigeon was an excellent flier that could reach speeds of 60 miles per hour, even the worst marksman could bring down 50 or 60 birds with a single shotgun blast. Also, taking young pigeons from nesting sites was extremely easy and profitable.)

Equilibrium points where $\frac{dP}{dt} = 0 = kP - \frac{kP^2}{N} - C$

$$0 = P^2 - NP + \frac{NC}{k} = (P - P_0)(P + P_0)$$

$$P_0 = \frac{+Nk \pm \sqrt{N^2k^2 - 4NkC}}{2k} = \frac{1}{2}\left[N \pm \sqrt{N^2 - \frac{4NC}{k}}\right]$$

$$P_0 = \frac{1}{2}N\left[1 \pm \sqrt{1 - \frac{4C}{Nk}}\right]$$

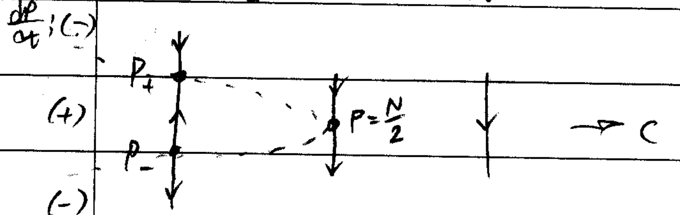
There are two equilibrium pts for $N^2 > \frac{4NC}{k}$ or $N > \frac{4C}{k}$ $\left(C < \frac{kN}{4}\right)$

Only one for $N = \frac{4C}{k}$

No equilibrium pts for $N < \frac{4C}{k}$, because P becomes complex.
$\left(C > \frac{kN}{4}\right)$

Bifurcations where $\frac{dP}{dt} = 0$ AND $\frac{d^2P}{dt^2} = \frac{df}{dt} = 0$ (p. 100)

$$\frac{d^2P}{dt^2} = k - \frac{2kP}{N} = 0 \text{ when } P = \frac{N}{2} \text{ (node)}$$



Phase lines → bifurcation diagram

$C < \frac{kN}{4}$ $\quad C = \frac{kN}{4}$ $\quad C > \frac{kN}{4}$: $\frac{dP}{dt} < 0$

↑

At node, $\frac{dP}{dt} = kP - \frac{kP^2}{N} - C = k\frac{N}{2} - \frac{k}{N}\frac{N^2}{4} - C = \frac{kN}{4} - C$

If $C > \frac{kN}{4}$, then $\frac{dP}{dt} = 0$ and population decays to zero (goes extinct).

So $C_{max} < \frac{kN}{4} = \frac{1}{4 \cdot 4} 5 \times 10^7 = \underline{\frac{5}{16} \times 10^7}$ pigeons per year is maximum sustainable harvesting rate

$c = 1.1 \frac{kN}{4}$

2. If the harvest rate was 110% of the rate in Part 1, how long would it have taken for the population to decline to 10,000, assuming that the initial population was near the carrying capacity of 50,000,000? $= N = P(0)$ $P(T) = 10^4$

Since we are starting near equilibrium, instead of trying to get an analytic solution to $\frac{dP}{dt} = kP(1-\frac{P}{N}) - c = kP - \frac{kP^2}{N} - c$, linearize about the equilibrium point $(P=N)$.

We found solutions to the equilibrium equation

$$0 = P^2 - NP + \frac{NC}{k} = (P-P_+)(P-P_-) \text{ where } P_\pm = \frac{N}{2}\left[1 \pm \sqrt{1-\frac{4C}{Nk}}\right]$$

but we are not near these eq. points.

Linearize the diffeq $\frac{dP}{dt} = -\frac{k}{N}(P^2 - NP + \frac{NC}{k})$ near $P=N$

Sec 1.9 #22 p. 136 (2.95)

Let $u = P - N$ $\rightarrow P = u + N$

$$\frac{du}{dt} = \frac{dP}{dt} = -\frac{k}{N}\left[(u+N)^2 - N(u+N) + \frac{NC}{k}\right]$$
$$= -\frac{k}{N}\left[u^2 + 2uN + N^2 - Nu - N^2 + \frac{NC}{k}\right]$$
$$= -\frac{k}{N}\left[u^2 + uN + \frac{NC}{k}\right]$$

small near equilibrium

$$\frac{du}{dt} \simeq -\frac{k}{N}\left[uN + \frac{NC}{k}\right] = -k\left[u + \frac{c}{k}\right] = -(ku + c)$$

natural decline due to competition for limited resources near carrying capacity — hunting

This makes sense.

Let $y = ku + c$

$$\frac{dy}{dt} = k\frac{du}{dt} = -k(ku+c) = -ky \rightarrow y(t) = y_0 e^{-kt}$$

$$u(t) = \frac{y-c}{k} = \frac{y_0}{k}e^{-kt} - \frac{c}{k}$$

t_0: pigeons at carrying capacity	t_1: time to decline to 10,000
$P(t_0) = P_0 = N = 5 \times 10^7$	$P(t_1) = P_1 = 10^4 = 50{,}000{,}000 - \underline{49{,}990{,}000} = N - \Delta P$
$u_0 = u(t_0) = P_0 - N = 0$	$u(t_1) = u_1 = P_1 - N = (N - \Delta P) - N = -\Delta P$
$y_0 = ku_0 + c = c = 1.1\frac{kN}{4}$	$y_1 = ku_1 + c = -k\Delta P + c = -k\Delta P + 1.1\frac{kN}{4}$
$= 1.1\frac{5\times10^7}{4^2} = 3{,}437{,}500$	$= \frac{1}{4}(-49{,}990{,}000 + 1.1\frac{5\times10^7}{4}) = -9{,}060{,}000$

(2) ... Find time (t_1) for P to decline to $P_1 = 10^4$, if $C = 1.1\,\frac{kN}{4}$

$$u(t_1) = u_1 = \frac{1}{k}\left[y_0 e^{-kt_1} - c\right] \quad \text{and } y_0 = c$$

$$u_1 = \frac{c}{k}\left[e^{-kt_1} - 1\right]$$

$$\frac{u_1 k}{c} + 1 = e^{-kt_1}$$

$$\ln\left(\frac{u_1 k}{c} + 1\right) = \ln e^{-kt_1} = -kt_1 \rightarrow t_1 = -\frac{1}{k}\ln a$$

where

$$a = \left(\frac{u_1 k}{c} + 1\right) = 1 + \frac{k\,4}{1.1kN}(P_1 - N)$$

$$= 1 + \frac{4}{1.1}\,\frac{P_1 - N}{N}$$

$$= 1 + \frac{4}{1.1}\,\frac{10^4 - 5\times10^7}{5\times10^7} = 1 - 3.64 = -2.64$$

$\ln(a<0)$ = error; we are too far from equilibrium for this method to work.

Analytic solution failed, so graph in Mathematica and calculate an APPROXIMATE numerical solution

Near the carrying capacity ($P \approx N$), the diffeq $\frac{dP}{dt} = kP(\underbrace{1 - \tfrac{P}{N}}_{\approx 0}) - c$ becomes $\boxed{\frac{dP}{dt} = -c}$ with a simple solution $P = a - ct$

Since $P(0) = N = a - 0$ the constant $a = N$ and

$P(t) \approx N - ct$. Now find T where $P(T) = P_1 = 10^4$

$$P(T) = N - CT = P_1 \rightarrow T = \frac{N - P_1}{c}.$$

$$= \frac{5\times10^7 - 10^4}{1.1 \times \frac{5}{16} \times 10^7} = 14.5 \text{ yrs}$$

This is a crude estimate, since we are NOT near ($P \approx N$) for long. Euler method better

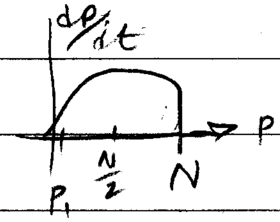
P_1

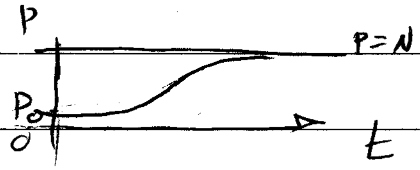
3. Once the population had reached 10,000, how long would it take to rebuild to $P_2 =$ 1,000,000 if harvesting were completely halted? (Note: Laws were passed in the mid-1800s to protect the passenger pigeons from hunting and trapping, but they were only really enforced once the birds became scarce.)

$N = 5 \times 10^7$

$\frac{dP}{dt} = kP(1 - \frac{P}{N}) - c$ $\to 0$ is simply logistic growth, as on

p. 10





Population will increase to carrying capacity if hunting stops and no other factors play in.

Find Analytic solution to $\frac{dP}{dt} = kP\left(\frac{N-P}{N}\right) = \frac{k}{N} P(N-P)$

$\int \frac{dP}{P(N-P)} = \int \frac{k}{N} dt$ This is separable, How to integrate?

Use method of partial fractions to write $\frac{1}{P(N-P)} = \frac{A}{P} + \frac{B}{N-P}$

NUMERATOR:

$\frac{1}{P(N-P)} = \frac{A(N-P)}{P(N-P)} + \frac{BP}{P(N-P)}$ $\to 1 = A(N-P) + BP = AN + P(B-A)$

$P^0: 1 = AN \to A = \frac{1}{N}$

$P^1: 0 = (B-A) \to B = A$

So $\frac{1}{P(N-P)} = \frac{1/N}{P} + \frac{1/N}{N-P}$ and

$$\int \frac{dP}{P(N-P)} = \frac{1}{N}\left[\int \frac{dP}{P} + \int \frac{dP}{(N-P)}\right] = \frac{1}{N}\int k\,dt$$

$$\ln P - \ln(N-P) = kt + \alpha = -\ln\frac{N-P}{P}$$

$$\ln\left(\frac{N-P}{P}\right) = -kt - \alpha$$

(3) Solution to $\frac{dP}{dt} = k\left(P - \frac{P^2}{N}\right)$:

$$\ln\left(\frac{N-P}{P}\right) = -kt - \alpha$$

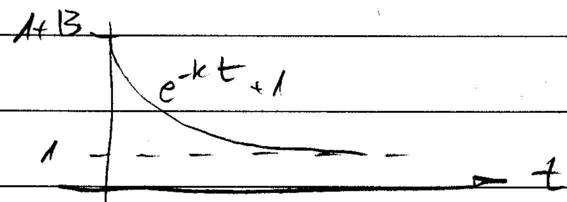
$$\left(\frac{N-P}{P}\right) = Be^{-kt}$$

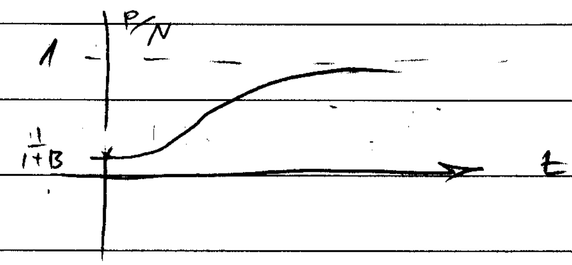
$P(0) = P_1$ IC: $\frac{N-P_1}{P_1} = Be^{0} = B = \frac{5\times 10^7 - 10^4}{10^4} \approx 5\times 10^3$

$$N - P = PBe^{-kt}$$

$$N = P(1 + Be^{-kt})$$

$$\frac{P(t)}{N} = \frac{1}{1 + Be^{-kt}}$$





Good - population P gradually increases to carrying capacity N.

t = time since hunting stopped (C=0)

Now solve for t_2 = time to reach $P_2 = 10^5$.

$$\frac{N-P}{PB} = e^{-kt} \rightarrow -kt = \ln\frac{N-P}{PB} = -\ln\frac{PB}{N-P}$$

$$t_2 = \frac{1}{k}\ln\frac{P_2 B}{N-P_2} \quad \text{where } \frac{P_2 B}{N-P_2} = \frac{10^6\, 5\times 10^3}{5\cdot 10^7 - 10^6} = 102$$

$$t_2 = 4 \ln 102 = 18.5 \text{ yrs } (+t_1)$$