

Sterile Insect Technique for the Elimination of Screwworm Flies

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Abstract

James Stewart includes an integral for the elimination of screwworm flies in the Partial-Fractions section (7.4, 8th Edition). Not only that, but he starts off the chapter on integration with a picture of a sterile male screwworm fly. Since Stewart failed to include a reference, I wondered where the integral of the exercise came from, so I undertook an interesting and enjoyable investigation....

1 Edward F. Knipling

The following is from an interesting book¹ I found, concerning sterile insect modeling:

Quote:

Knipling produced a simple numerical model that foreshadowed most future modelling developments (Knipling 1955, 1959). The central feature of Knipling's model, and one found in almost all subsequent models, is the ratio of fertile males to all males in the population: $(M/(S+M))$ where M is the number of fertile males (or females, assuming a 1:1 sex ratio) and S is the number of sterile males. This gives the proportion of the population, under ideal conditions, that results in fertile egg production as a result of some fertile females mating with fertile males. Knipling's (1955) model for the release of sterile insects was a simple modification of the geometric model

$$N_{t+1} = \lambda N_t$$

using the sterility factor above:

$$F_{t+1} = \lambda F_t \left(\frac{M_t}{S + M_t} \right)$$

End quote.

You'll notice that the equation $N_{t+1} = \lambda N_t$ is like the interest problem we talked about in class at one point: the principal in the bank at time $t + 1$, N_{t+1} , is equal to $(1 + r)N_t$. (So in Knipling's formulation, only a fraction of those dollars go back into your account (some of the dollars are spent each time).) These equations generate **sequences** of values, representing populations for all (integer) time.

"It was observed that a female screwworm fly mates only once in her life." [1] So only that fraction of females which mate with fertile males will contribute offspring – the rest don't contribute. I hope that makes sense. This biological feature of the screwworm lends a certain degree of credibility to the Knipling model: only that fraction of females (equal to the fertile proportion of the male population) reproduces; the others fail to reproduce because they've mated with unproductive males.

¹Sterile Insect Technique: Principles and Practice in Area-Wide Integrated Pest Management

2 Stewart's Calculus Problem

Here's Stewart's calculus exercise:



Sterile insect technique One method of slowing the growth of an insect population without using pesticides is to introduce into the population a number of sterile males that mate with fertile females but produce no offspring. (The photo shows a screwworm fly, the first pest effectively eliminated from a region by this method.) Let P represent the number of female insects in a population and S the number of sterile males introduced each generation. Let r be the per capita rate of production of females by females, provided their chosen mate is not sterile. Then the female population is related to time t by

$$t = \int \frac{P + S}{P[(r - 1)P - S]} dP$$

Suppose an insect population with 10,000 females grows at a rate of $r = 1.1$ and 900 sterile males are added. Evaluate the integral to give an equation relating the female population to time. (Note that the resulting equation can't be solved explicitly for P .)

By the way: Stewart's notation is less than desirable: it would be better to use $\lambda = (1 + r) = 1.1$ like the interest problem. r frequently designates a rate of increase (or decrease).

3 Truth and Reconciliation

So how do we make these two different approaches agree? The Knipling model seems a little more intuitive. Let's see how we can turn it into Stewart's integral.

First of all, assuming the 1:1 ratio of males to females among offspring, referenced above, then F_t is the same as M_t in Knipling's formulation. Hence

$$F_{t+1} = \lambda F_t \left(\frac{F_t}{S + F_t} \right) \quad (1)$$

This is called a "difference equation" for F , and represents the (female) population in generation $t + 1$, based on values from preceding populations (in this case only the previous generation's population – so we call this "first order" – it only involves the previous generation, assumed to occur at time t).

By the way, the focus on females is interesting, but actually terribly important. Do you realize that males are relatively useless? 100 males on an island and 1 female, and the population will crash; but 1 fertile male and 100 females, and the population will flourish (inbreeding aside). Males are over-rated (sorry guys! Kind of ruins your Valentine's Day, right?).

I'm going to rewrite equation (1), making use of my favorite trick in the book (adding the appropriate form of zero) for my own nefarious purposes:

$$F_{t+1} = \lambda F_t \left(\frac{F_t + S - S}{F_t + S} \right)$$

Therefore

$$F_{t+1} = \lambda F_t \left(\frac{F_t + S}{F_t + S} - \frac{S}{F_t + S} \right) = \lambda F_t - \lambda F_t \left(\frac{S}{F_t + S} \right)$$

Let's focus instead on the **change** from generation to generation: i.e., let's subtract F_t from both sides, and rewrite this as

$$F_{t+1} - F_t = \lambda F_t - F_t - \lambda F_t \left(\frac{S}{F_t + S} \right)$$

Now, we should recall an important approximation: that

$$f(t+h) - f(t) \approx h \frac{df}{dt}$$

This comes from “discretizing” the derivative – as given by the limit definition – by simply dropping the limit:

$$\lim_{h \rightarrow 0} \frac{f(t+h) - f(t)}{h} = f'(t) = \frac{df}{dt} \approx \frac{f(t+h) - f(t)}{h}$$

Ordinarily I urge you to not be a “limit-dropper”, but there are times to drop limits...:) There are, however, never any times to drop a dx from an integral – just to be clear!

Hence

$$F_{t+1} - F_t \approx 1 \frac{dF}{dt} \approx \lambda F_t - F_t - \lambda F_t \left(\frac{S}{F_t + S} \right)$$

and so (dropping the subscript t on F – just think $F = F(t)$)

$$\frac{dF}{dt} \approx F(\lambda - 1) - \lambda F \left(\frac{S}{F + S} \right) \tag{2}$$

Treating the quantity on the left as a quotient of differentials (which we do if we think like physicists – another reason not to drop them!), we can rewrite equation (2) as

$$\frac{dF}{F(\lambda - 1) - \lambda F \left(\frac{S}{F+S} \right)} \approx dt$$

Multiply top and bottom of the left-hand side by $F + S$, to clear that nasty denominator, to get

$$\frac{(F + S)dF}{F(\lambda - 1)(F + S) - \lambda FS} \approx dt$$

so that

$$dt \approx \frac{(F + S)dF}{F(\lambda - 1)(F + S) - \lambda FS}$$

Simultaneously factoring and expanding the denominator, we get

$$dt \approx \frac{(F + S)dF}{F [(\lambda - 1)F + (\lambda - 1)S - \lambda S]}$$

and, finally, that

$$dt \approx \frac{(F + S)dF}{F[(\lambda - 1)F - S]}$$

To make things look more Stewart-esque, change notation F for P to yield

$$dt \approx \frac{(P + S)dP}{P[(r - 1)P - S]}$$

and then integrate to get the time elapsed (Stewart's integral):

$$t = \int dt \approx \int \frac{(P + S)dP}{P[(r - 1)P - S]} \quad (3)$$

Whew! This equation (3) is Stewart's integral.

Notice that, as things stand (and as Stewart said), P is an **implicit** function of time: $P(t)$. When we solve the integral on the right for P , we'll have $P(t)$, but not explicitly.

4 Solution

This problem appears in Stewart's section on partial fractions, so we may as well use partial fractions to compute this integral...;) Using partial fractions (distinct linear factors) to rewrite the rational integrand, we get

$$t = \int dt \approx \int \frac{(P + S)dP}{P[(r - 1)P - S]} = \int \left[-\frac{1}{P} + \frac{r}{P(r - 1) - S} \right] dP$$

Then integrate to obtain

$$t = -\ln(P) + \frac{r}{r - 1} \ln |(r - 1)P - S| + C$$

We don't need an absolute value on the $\ln(P)$ since P is always positive. But we do need to worry in the event that $(r - 1)P - S = 0$ (i.e., $P = \frac{S}{r - 1}$).

If we know the initial population $P(0) = P_0$ (that is, the population at time $t = 0$), then we can solve for C :

$$0 = -\ln(P_0) + \frac{r}{r - 1} \ln |(r - 1)P_0 - S| + C$$

i.e.,

$$C = \ln(P_0) - \frac{r}{r - 1} \ln |(r - 1)P_0 - S|$$

Hence

$$t = \ln(P_0) - \ln(P) + \frac{r}{r - 1} \ln |(r - 1)P - S| - \frac{r}{r - 1} \ln |(r - 1)P_0 - S|$$

or, using all those log properties you learned recently,

$$t = \ln \left(\frac{P_0}{P} \right) + \frac{r}{r - 1} \ln \left| \frac{(r - 1)P - S}{(r - 1)P_0 - S} \right| \quad (4)$$

So what we have here is $t = g^{-1}(P)$, whereas what we would really like is $P = g(t)$. That means that we have the inverse function of the function we actually desire. In the following figures (1) and (2) I graph this function $t = g^{-1}(P)$ under two different scenarios:

- with the parameters Stewart specified, i.e. $r = 1.1$, $P_0 = 10000$, and $S = 900$; and
- with $S = 1500$, and all other parameters the same.

Figure 1: With parameters $r = 1.1$, $P_0 = 10000$, and $S = 900$, the screwworm population continues to grow. At left, $t = g^{-1}(P)$; at right, $P = g(t)$ (by reflection).

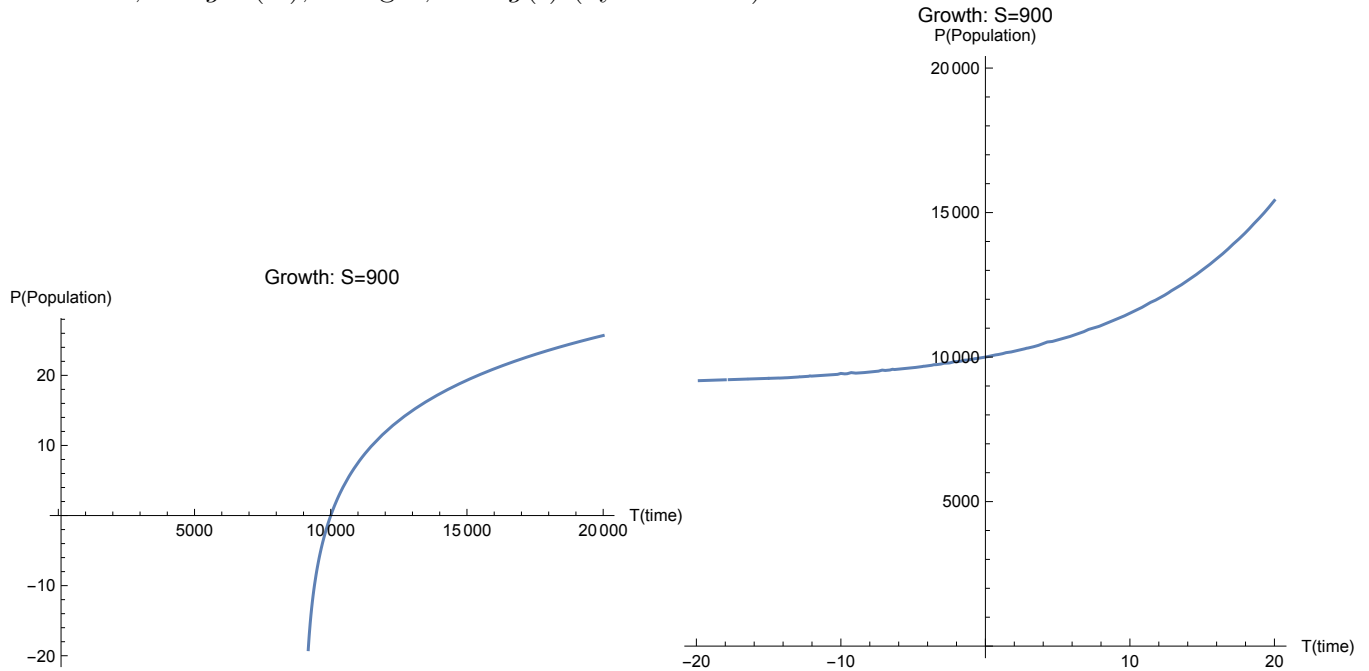
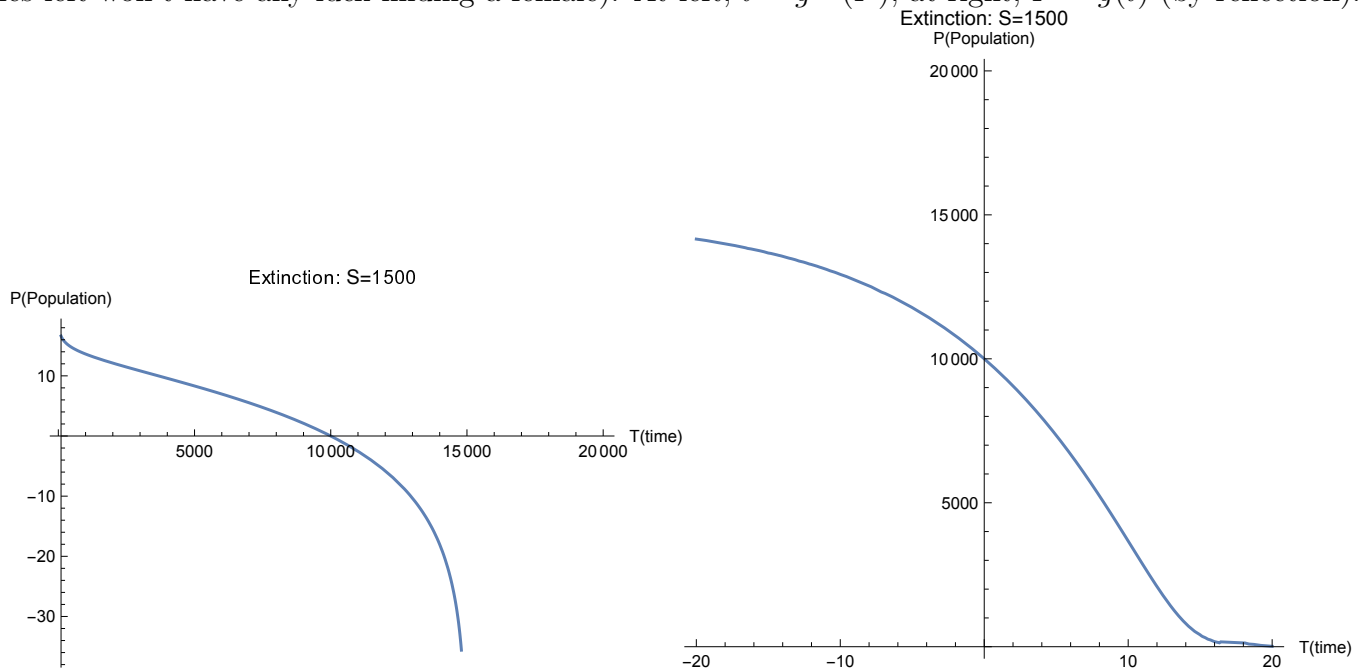


Figure 2: With $S = 1500$ sterilized males introduced, the screwworm population dies out (well, **asymptotically**: from the biological standpoint, we anticipate that, when numbers get small, the poor few fertile males left won't have any luck finding a female). At left, $t = g^{-1}(P)$; at right, $P = g(t)$ (by reflection).



The graphs on the left seem a little odd, but that's because I'm plotting the inverse function $t = g^{-1}(P)$, rather than $P = g(t)$. To get $P = g(t)$, we simply reflect the graphs about the line $t = P$ to put time on the “ x -axis” where we would usually expect it, and then $P(t)$ on the “ y -axis”, where we think it belongs.

These graphs of the two different cases suggest something else interesting, and important: 900 sterile males isn't enough; 1500 is perhaps too many. Since sterile flies cost money, this begs the question: “What is the optimal number of flies that will get the job done?” The particular number of flies where the behavior of solutions changes leads to a **bifurcation** (dramatic change) in the solution.

Mathematics is frequently called upon to determine these optimal “Goldilocks” solutions: the porridge is neither too hot, nor too cold – but rather “just right”. Can you figure out what value of S – sterile males – determines whether the population disappears or takes off?

It's actually fairly easy for the difference equation (1): is it the same for the **continuous** solution of Stewart's integral, equation (4)? For the answer, you might look to the derivative of F , equation (2).

5 For more details....

- a. Featured Creature: *Cochliomyia hominivorax*
- b. Mathematica file for the figures

References

- [1] S. C. Smith. A guide for the eradication of screwworms. Technical report, The Mexico - United States Commission for the Eradication of Screwworms, 2009. Accessed by ael at <http://www.flisart.org/screwworm/Screwworm%20Eradication%20Guide%20Print%20Version.pdf>, 2/11/2019.