Age and Stage Structure with Sensitivity Analysis

Tony Starfield

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Thanks to Terri, we now have a population model on a spreadsheet. Again, notice it looks quite complicated, but it wasn't as difficult to put onto the spreadsheet as you perhaps thought it was going to be. And it's fairly simple to understand how you used your three equations in the model.

We still are faced, now that we have this model, with the things that we don't know. We've put in reasonable guesses for the calf survival rate and for the calving interval. But we still don't have a reasonable estimate for the adult survival rate, and we've completely guessed at the initial age structure.

What we need to do now is some detective work. We are going to calibrate our model in the sense of trying to get at the parameters or the starting values that we didn't really know. And this is pretty much a Sherlock Holmes-type operation.

And, perhaps, the first thing Sherlock Holmes would say is, "Are there any clues that we are missing? Is there anything that we haven't yet used? Have we used everything we know?" And the answer is, "No," because if you think about it, I rather casually, right at the beginning when I was describing the problem in the Kruger Park, told you how many elephants they had been removing each year. And you might recall that, on average, they were removing about 400 elephants per year. If you think about that, if they had to remove 400 elephants per year, that tells you that those 7,000 elephants were increasing by 400 in the space of one year, on average. What are the implications of that?

Let's write down these numbers and have a look at them. So 400 out of 7,000 elephants, as a percentage if you do the calculation, is approximately 5.7 percent. So that means, on average, the elephant population is growing at 5.7, somewhere between 5.7 and 6 percent per annum, which, by the way, is a reasonable rate for a large mammal.

When you see that the population is growing at 5.7 percent per year in the real world, that tells you why it was useful in the spreadsheet that Terri developed to calculate a growth rate. Remember, the growth rate lambda was the total population at time T plus 1 divided by the total population at time T. And that should come out to be 1.057.

Well what did it actually come out to, and what exactly are we talking about here, because if you remember, we've been graphing lambda? And what happens when you graph lambda is that you get something that might end up looking rather like this, perhaps. Basically, what happens is that lambda fluctuates and then settles out at a constant value. And that constant value at which it settles out is reported on your spreadsheet as final lambda. And it is that final lambda that should turn out to be somewhere close to 1.057, okay.

Well let's ask questions about what affects that value of final lambda and how it relates to the two things we don't know - the initial age structure and the adult survival rate. So let's do an experiment on the spreadsheet.

Suppose we went and changed the initial age structure in some fairly dramatic way. Suppose, for example, we doubled all the numbers we had put in at time T equals 0 for age classes 10 to 20. And if you did that, I'm not sure exactly what you'll see. You can look at this on your own spreadsheet. But what you would've noticed is that maybe the first part of the diagram changed, but if you looked at the final value of lambda, you will have noticed that it wasn't changed by doing that experiment. And you can continue experimenting with changes in your initial age structure, and you will continue to notice that all that the change in initial age structure does is affect this fluctuating part of lambda. But no matter what you do to the initial age structure, the final value of lambda remains constant. That's very interesting.

Well if changing the initial age structure won't change lambda, won't change the final value of lambda, what will change the final value of lambda?

Well, change your adult survival rate. And if you do that, you will notice immediately that it affects the final value of lambda.

So now we have an approach to the problem. The first part of that approach is that we need to choose a value for the adult survival rate in order to get a final value of lambda that is close to 1.057. And you're going to see shortly how to do this on a spreadsheet. Or there's nothing to stop you from taking your own spreadsheets and looking at that right away. But that 400 out of 7,000 that led to 5.7 percent is our clue that tells us how to choose the adult survival rate.

Incidentally, if you were to do more of a sensitivity analysis, you would find that changing the calving interval will also change the final value of lambda and so will changing the calf survival rate. So if, at any stage when you do a sensitivity analysis, you change, for example, the calving interval, you need to double check that you are using a value for the adult survival rate that leads to a final value of lambda that is plausible. And what do we mean by “plausible?” Something like 1.057 as a value.

What we have done here, just by playing with our spreadsheet, is we’ve discovered a theorem that was published by a British mathematician called Leslie around about 1942. Leslie, using matrices, was able to show that in a deterministic age-structured model, two results. The first result is that the initial age structure affects only the way in which the population changes in the short term but has no impact on the growth rate of the population in the long term. And the second result is that the value of the growth rate in the long term depends only on the demographic parameters of the model, in other words, survival and fecundity rates.

Now if you’ve taken a class in matrices, and if you understood concepts like dominant eigenvalues, then you would’ve been able to prove this mathematically. And I don’t want to discourage you from doing that. In fact, I encourage you to do it. But notice how you could reach the same conclusion just by sensibly performing experiments on the spreadsheet model. I want to stress that this is only true for a deterministic model. In a stochastic model, all bets are off.

Okay. So we’ve figured out how to calibrate our adult survival rate. And we’ve also figured out that we don’t need, in a sense, to worry about what the initial age structure is, provided we are running our model long enough in order to be able to get to that steady value of lambda, that point at which lambda no longer changes over time.

So we’ve calibrated our model. In a sense, we were lucky here. The heuristic to push on, regardless, paid off. But almost always, one ends up being lucky because by pushing on, regardless, and having an actual working spreadsheet to play with gives you the insight to, if not answer completely what the calibrated values of your parameters are, it at least gives you the insight to understand how they influence your results. And what might be reasonable guesses and what might be reasonable levels of accuracy that you need. So, press on regardless, get a spreadsheet working and do a sensitivity analysis.

We’re going to look at how to do this on a spreadsheet in a moment. Terri’s going to take you through what we’ve talked about here. But before we do that, I’ve got a question for you. What is the current age structure of the elephants in the Kruger Park? Think about that for a second.

Well, if you were able to highlight it, you will notice that when lambda reaches a steady value, if you actually looked at the proportion of animals in each age class, that doesn’t change with time. And remember, the managers in the Kruger Park have been managing that elephant population for about 30 years, which is a long period of time in a way that does not change the age structure. So we would expect the current age structure to be the age structure that we find at the end of our spreadsheet. Let’s have a look at how this looks on a spreadsheet.

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