Age and Stage Structure

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It's time we looked at a real problem. And so in this module, we're going to see how a population model could be used to help decision-makers make a decision about a real practical problem. And the problem we're going to look at relates to elephants and takes place in one of my favorite places in the world, the Kruger National Park in South Africa.

Let me tell you something about the Kruger National Park. It's an area of about 7,000 square miles, in fact, a little over 7,000 square miles. And if you think about that, that's bigger than the state of Massachusetts. It's bigger than Switzerland. It's an area that was fenced in in the 1950s. And we'll talk about the implications of that in a moment. The park itself was created in the 1890s, which makes it one of the oldest national parks in the world. And was based, pretty much, on the ideas that went into the development of Yellowstone.

As I said, in the 1950s, it was fenced in, and the fence was elephant-proof, or for the most part, was elephant-proof. At that time, the elephant population was growing. It was growing, but it was also dispersing through the park into areas where elephants had been wiped out many, many years before. As it grew, it became and more and more a matter of concern to the people in the Kruger National Park, and the reason for that is that large herbivores are capable of changing their vegetation. And by changing the vegetation, they change the habitats for other species. So there was a concern that the elephant population was growing to a point where, not only was it pushing down a lot of trees that looked unsightly to some people, but it was also potentially having an impact on the numbers and, in general, the biodiversity in the whole of Kruger Park.

This is a problem that's been described as the problem of local over-abundance of endangered species, or of protected species. And the idea is that you have species where you are trying to keep the population as high as possible, but in the areas in which you conserve them, the population densities get to be too high.

The heuristic that was developed throughout Africa with relation to elephants was that a density of about one elephant per square mile was a good density to have. "Good" is a very subjective word. What do we mean by “good?” Probably the answer is that one elephant per square mile in most African habitats produces a vegetation that is attractive to the human eye, probably has very little to do with bio-diversity, per se.

Nevertheless, on the basis of this heuristic, the management of Kruger National Park developed a control mechanism for elephants that they implemented for over 30 years. And this is how it worked. Every single year, they counted the elephant population. In other words, for two weeks, they ran an aerial census over the entire 7,000 square miles of the Kruger National Park and so, they believed, counted every single elephant precisely.

And if they found there were more than 7,000 elephants, then they removed - and for the word “remove,” substitute “kill” or “cull” - the excess. So, for example, if, in a particular year, they counted 7,200 elephants, they would actually kill 200 elephants that year. Now the way in which they killed those elephants turns out to be important.

The sex ratio of elephants in the Kruger Park is approximately 1 to 1. So half of the elephants would have been male, and half of the elephants would have been female. And in the process of removing elephants, they removed equal numbers of males and females. So they would kill 100 males and 100 females.

Now the way elephants group and congregate in the Kruger Park is also important because it turns out that there are breeding herds that might be quite large. And these breeding herds are usually under the control of an elderly matriarch and consist of females and young males, up to the age of puberty. And then all males above the age of puberty wander around away from the breeding herds in groups of - they might be solitary - there might be two or three or four in a group.

They would round up a whole breeding herd from the air, dart them, not to kill them but to put them to sleep, then land on the ground and kill the entire breeding herd. And in the process, they would count how many females they killed and how many males they killed. So, for example, suppose they had reached the point where they had killed 100 females within breeding herds and also, perhaps, killed 20 young males in the process. They would then go out and target an additional 80 males to make up their quota of 100 males. And, as I say, they did this year after year for 30 years.

And the implication of them doing it in this way is, one, that they maintain the sex ratio, and, two, if you think about it, they maintained the age structure of the female population because they were killing whole groups at a time. They weren't targeting individual females. And, as I said, they did this for 30 years. And, on average, in this way, they removed about 400 elephants a year.

Now with time, it turned out that killing elephants, for whatever reason, was beginning to be unpalatable to people interested in conservation and interested in animal welfare throughout the world. And management of the Kruger Park started, rather desperately, to look for alternatives to actually having to kill elephants. You can't exactly carry 400 elephants a year to some other place.

And what they came up with as a possible solution to the problem was a contraceptive dart. It was a dart that could be put into a rifle and shot from a helicopter into a female, and on impact, it would inject the contraceptive into the female. And the contraceptive was supposed to be capable of preventing that female from breeding for two years. The actual way the dart worked was to prevent the fertilized egg from attaching itself to the side of the womb.

So this became a fairly serious alternative paradigm for management. And one of the questions that arose was how many females would they have to dart every year to replace - if you like, the 400 on average - animals that they were removing every year. Or to put the question differently, how many females would they have to dart every year in order to keep the entire elephant population constant?

And when people were asked to guess at an answer to this, they came up with numbers like maybe 5 percent of the breeding females. Some people came up with 10 percent. A few people came up with 15 percent, but generally speaking, a consensus was developed among experts that, probably, you would need to dart about 10 percent of the breeding females every year. But some corroboration of that number was needed. And it was suggested that maybe a way to do this was to develop a model. And, as you're going to see, the models show that the expert opinion was way out of line.

So we now see where a model might be useful in helping people decide where this paradigm of darting elephants is a feasible paradigm. Is one going to actually be able to put it into practice? So we now turn out attention to building a model. And if you think about it - and this is true of all problems when you're dealing with real issues - there are lots of complicated things to consider.

And, in particular, there are lots of complicated issues that arise with the whole process of darting. For example, you might ask questions like, "What's the possibility that you're going to dart the same female twice within a two-year period?" You could ask, "What happens if you dart a female who's already pregnant? What happens if you dart a female who isn't part of the breeding herd? In other words, she's too young to breed? What happens if you dart males instead of females, by mistake? What are the chances that if you hit the female, the dart will actually do what it's supposed to do"? These are quite apart from the issues about how elephants breed and how elephants congregate and so on.

And one other way to deal with messy, real-world problems is to divide and conquer. That's always a useful heuristic. And in this particular case, it's useful to divide the issues relating to how management is implemented from the issues that relate to the actual population itself. And, if you think about it, if you could ignore anything to do with darting and calculate what might happen if darting worked perfectly, you could then modify your answer if you needed to by, perhaps, doing a separate darting model.

So what we are going to do is we are going to rephrase the question. Instead of asking the question, "How many females do we need to dart every year to keep the population constant," we're going to remove darts from the whole question, and we're going to ask the question, "What percentage of adult - and for adult mean 'breeding' - females should be prevented from breeding in order to keep the population constant? What percentage of adult females need to be prevented from breeding in order to keep the population constant?"

And to do that, we need to build a population model. Well I jumped to a conclusion there. I said, "We needed to build a population model." A good heuristic is that if you've got a management issue related to a population, don't try and answer that question in the kind of way in which you would've dealt with a question, a word problem that you were given in high school. Don't try and get directly at the answer. A sensible thing to do is to develop a suitable population model and then manipulate that model in order to get at the answers you want.

So what we are going to need to do is actually design an elephant population model. And if we can get that elephant population model working in a realistic way, we can then figure out how to stop the females from breeding and then ask the question, "What proportion of the breeding females need to be prevented from breeding in order to keep the population constant?"
So we are now going to develop an elephant population model with that goal in mind. And in designing our model world, we need to think about the issues that need to be addressed when you develop an elephant population model, or very often, when you develop any management, animal-management model. Let's run through some of those.

For example, you might ask, “Do we need a deterministic model or a stochastic model?” And remember the heuristic? You don’t want to go for a stochastic model unless it’s absolutely essential.

You could ask, “Do we need a spatial model?” We haven’t talked about spatial models yet, but would it be useful, in this case, to break the population up into distinct groups, distinct spatial areas?

Do we need to include density dependence into our model? That’s always a good question.

Do we need to model males as well as females, or to rephrase that, are males really necessary? And surprisingly often when, in the modeling world at least, you don’t need to worry about the male population.

And then, finally, we need to think about how we’re going to actually present the population. And it turns out there are a number of ways in which we could do this. For example, if you think about the Roc population, originally, we had this variable R for Roc, R subscript T. We looked at the total population, and we looked no further into the details of the population. So could we look at the total elephant population, or could we model the total female elephant population? Is that a good way to design our model?

Alternatively, we might want to break the population up into life stages. For example, we might want to look at juveniles versus adults. Is that a useful way to represent the elephant population?

Or we might want to go into even more detail and divide it up into age classes. So we might have an age-structured model where, perhaps, we’d look at elephants age 0 to 1, 1 to 2, 2 to 3, 3 to 4, and so on.

Or, if we really wanted to go the whole hog, or maybe the whole elephant, do we want an individual-based model, such as the model that we developed when we had two Rocs in Saudi Arabia? Except this time, we have 7,000 elephants. Do we want to model 7,000 individuals? And even if we ignore males, do we want to model 3,500 individual females?

These are the issues you need to address, bearing in mind the objectives of the model and probably influenced by what you know about elephants. And at this stage, you know, or might know very little about elephants.

So this would be a good time to take a break, for you to go away and come back with a list of questions to ask about elephants, not about darts. Remember, we've cut darts out of this problem. But come back with a list of questions that would help you design your model world, bearing in mind the issues that we've just been talking about.

PAUSE the video: Create a list of questions about elephants.

Well, I wonder what you have on your list of questions. How many of you cheated and asked questions about the darting process? Remember, we don't see darts in our model world at this stage. Well I have a number of things that you might've asked, and I'm going to try and answer them for you.

The first item on my list is the age of first reproduction. And the answer to that is probably about 12. Now the gestation period for an elephant is 22 months. So there's some uncertainty about when you're talking about 12, whether that's the age at which conception occurs or the age at which a calf is born. But for all practical purposes, you can count all females aged 12 and up as part of the breeding adult population.

Then, perhaps, you had a question about fecundity. People talk about something called the calving interval. That's the time between the birth of one calf and the birth of the next. And the calving interval is in the range of 3.1 to 3.3 years. And that's been corrected to include the affect of, occasionally, a female having twins. So somewhere, every 3.1 to 3.3 years, a female will produce a new calf. In other words, about one calf every three years.

Survival rates. Well the calves - and when you talk about the calf survival rate, you're thinking about the number of calves that survive from newborn to age 1 - is somewhere in the range of .8 to .9. So 80 to 90 percent of newborn calves live to be one year old.

All other elephants one doesn't really have a number for. And all people can tell you is that it's very high. And by very high, they probably mean greater than .9. And probably once you've survived that first year, your survival rate doesn't vary from one year to the next. In other words, you have as much chance of living from 2 to 3 as you have if you were an elephant of living from 53 to 54 until you drop dead at what age? A maximum age, if you want to think about that, if you haven't died already, is probably 60. So you can assume that all elephants that get to reach age 60 don't live to 61.

Maybe you're wondering whether there's a drop off in fecundity as you approach 60. And the answer is there's a bit of evidence that they might be. But it's such a small effect, and you have very few females aged 55 to 60 anyway that I wouldn't worry about it.

Perhaps you asked about the sex ratio. Well we've already talked about that. It's 1 to 1.

If you were really smart, you might've asked what the age structure is of the current population. That's a really good question. Unfortunately, the answer is, "We don't know." As far as I know, nobody has tried to keep records on that.

Did you ask about the effect of rainfall on the population? There doesn't seem to be an effect. In areas where they are very high density, something like four or five elephants per square mile, there's been some correlation between the calving interval and rainfall so that fewer calves are born in droughts. But we're getting nowhere close to that kind of density.

With Rocs in mind, you probably asked about disease. Is there an elephant flu? The answer is, "Not that we know of."

Then you might've had some other questions, which get more to the point of the problem. Perhaps you asked, "What proportion of females are breeding females?" Well that's a catch question in the sense that if we knew that, this would be a very, very easy problem to solve. Unfortunately, we don't know what proportion of females are in the age classes 12 to 60. That's something we're going to have to find out using our model.

And we've got to be a little bit careful there, too, because if we did know what proportion are in the age class 12 to 60 now, does that mean the same proportion are going to be in the age class 12 to 60 when contraception is applied, when some of them can't breed? Think about the effect of contraception. It changes the age structure of a population. Just look at the difference, for example, at the age structure in, say, the United States versus the age structure in the Congo.

Maybe you wanted to know more about how elephants actually breed. For example, do they pair off? And the answer is, "No." What happens is that when a female is reproductive and needs to breed, she sends out very low-frequency messages to the males saying, "Come and get me. Come and get me." And these messages spread out over long distances. And the more active males, the stronger males, will come and breed with her. So you need very few males to actually produce the offspring.

That's about it on the list of questions that I've had. Do you think those answers are going to help you to design your model? Let's go back to the questions you need to address now because the next thing we're going to do is take a break, and I'm going to actually ask you to answer these questions.

And if we go back to the list we looked at earlier, you've got to decide on a deterministic or stochastic model. You have to decide whether we need a spatial model. Do you want to include density dependence, or should you include density dependence? Are males necessary? And then, finally, how are you going to represent the population? And I'd just like to talk to you a little bit about the implications of that before you go away and think about it.

I want to draw the distinction between two technical terms. We've used the word "parameters" already, and we've occasionally used the word "variables." What's the difference between a variable and a parameter?

A **parameter** is something that you usually have data for. It's usually something like a birth rate. So all the numbers that I've given you, like calving interval and the survival rate of calves, those are all parameters.

Variables are the things that you calculate in the equations in your model. So, for example, in the Roc model, when you said, "R-T plus 1 equals C times R-T," C was a parameter, and R was a variable.

Now if you are looking at - let's suppose, just to make this easy, that you've decided not to include males. If you look at the options for representing the population, if you go with the total population, you only need one variable for the females, and that's the total number of females.

If you go to the life stages, and you introduce two or three life stages, then you're going to need two or three variables. If you go to an age-based model, and you have age classes 0 to 1, 1 to 2, 2 to 3, all the way up to 59 to 60, you're going to have to have 60 variables that you update at every time step. And if you go to an individual-based model for 3,500 females, you're, in a sense, going to have 3,500 variables. So you decide how you're going to represent the population.

And while you're doing that, think also about the time step of your model. Is it going to be one year, one week, ten years? Why don't you go away, try to answer these questions, and then we'll talk about your answers and develop our model in the next segment.

PAUSE the video: Determine how you will represent the population.

Now we are going to answer those questions and develop our model world and our model. Deterministic or stochastic? No good reason to go to stochastic, is there? If rainfall had been important, we might have done that. But nothing tells you, you'll need a stochastic model. There weren't even questions that related to space, so nothing tells you that you need a spatial model. Density dependence? We're trying to keep the population at a fixed value, so the density isn't changing. No need for density dependence. The parameters that we develop for the model, the data we got on calving interval and survival rate were all obtained for the current population of about 7,000 elephants. No need to worry about density dependence. Males? Unnecessary.

So the key question is how do we represent the population? And it's pretty obvious we can't go for total population, and when I say, "population" now, I mean female population because we're ignoring males. We can't go for total population because we don't know what proportion are breeding females. So that won't work.

We wouldn't really want to go to an individual-based model here unless there was a really good reason for it. What would constitute a really good reason? Well one would be that maybe the breeding behavior of elephants changes if they are prevented from breeding, or something happens where an individual's behavior becomes a really important part of the model. And I don't think there's any need to do anything like that.

So that leaves two options: The age-based model and the life-stages model. And I suspect most of you, very logically, went for the life-stages model. And some of you might've gone for two life stages, and some of you might've gone for three. And what I'm going to do is show you what a three life-stage model might look like, and then I'm going to tell you why it was a bad mistake to go for it.

So if we could have a look at a conceptual diagram of what a three life-stage model might look at, my three life stages would be calves age 0 to 1, juveniles age 1 to 12, and adults age 12 and up. And the time step I would go for is one year. Some of you might've suggested two years because of the dart, but remember, we're not talking about darts. And it always makes sense in population models unless there are good reasons to go with a time step of one year.

So time T is, if you like, this year, and time T plus 1 on the diagram is next year. And we're going to ask, “Where did the juvenile at time T plus 1 come from”? And the answer is they are calves at time T. So I’m going to draw an arrow, which says that those calves at time T that survive will become juveniles at time T plus 1. That’s very clear, simple.

But there are also some juveniles that will still be juveniles at time T plus 1. So there’s also an arrow from J at time T to J at time T plus 1.

On the other hand, some of the juveniles will, as it were, graduate into adults. They will turn 12, and they will go from juveniles to adults.

A lot of the adults in the age classes 12 to 60 are going to still be adults if they survive. But some of them are going to hit 60 and fall off the map, drop dead.

And, finally, we have to ask the question, “Where do the calves come from?” And the answer is, “They come from the breeding adults and all the adults, because they’re age 12 and over, are breeding.” They come from the adults at time T plus 1.

Some of you might have wanted to draw that arrow from A at time T to C at time T plus 1. But if you think about it, a female has to be alive to give birth. And so it’s not a good idea to go from A at time T.

So that’s your conceptual model. And what’s wrong about the conceptual model, or what causes difficulty is that there are two arrows going out of J and two arrows going out of A. And the question you have to ask is, “What proportion of juveniles are going to graduate to adults, and what proportion of adults are going to hit the age of 60?” And those are not easy questions to answer.

They’re not easy to answer because even with a very high survival rate, you will find that the number of 11 to 12 year olds is not the same as the number of 1 to 2 year olds in a population. And even if it were the same, you’d be in trouble because, as I said earlier when we were talking about whether to go with an individual-based model or an age-structured model, if you knew the proportion that are going to switch out of juveniles to adults now, that wouldn’t help you when you introduce contraception. When you prevent females from breeding, you’re going to change the age structure. And so the number of animals aged 11 to 12 is going to change. And the same is going to be true at 59 to 60. So you can’t guess at the proportion of juveniles that will become adults because that guess will change as you change the proportion that can breed.

Now I've got nothing against guessing in a model. If you're going to guess at a parameter you don't know and then do a sensitivity analysis to see what difference it makes, that's perfectly okay with me. But if you're going to guess at something that changes because of the experiment you're doing with the model, and you're now going to guess at how it changes, then you might as well not build a model. So there's a fatal flaw in going to a stage-structured model here, and that is that you can't determine what proportion of juveniles become adults in a particular year and what proportion of adults go from age 59 to 60.

So we're going to have to drop that idea. In a sense, I put it there to trap you to show you how you might've gone in that direction and might even have guessed at something and might've made a reasonably good guess, but you would never have realized that that guess was actually undermining your whole thought experiment.

What does that leave us with? It leaves us with an age-structured model. Let's have a look at a conceptual model for age-structured models.

Well here at time T, we have 60 age classes, starting from 0 for a newborn calf, through to 59 for an animal that has just turned 59. That looks like a lot of variables, doesn't it? But let's have a look at what happens as we go from time T to time T plus 1. If you think about it, the one year olds at time T plus 1 are the zero year olds that survived their first year. There's the arrow. The two year olds at time T plus 1 are the one year olds. The three year olds are the two year olds at time T. Three goes to four, and so it goes until 57 goes to 58, 58 goes to 59, and unambiguously, 59s drop dead on their 60th birthdays.

Look how beautiful that is. No ambiguity. An arrow goes from one circle to the next at time T plus 1, and you don't have to argue about what proportion is split between, say, one circle and the next.

And now we have to figure out how many newborn calves we've got, and there are your adult breeders at time T plus 1. And they are going to produce the newborn calves.

And so, although the age-structured model looks much more complicated, it is, in fact, simpler than the stage-structured model because the arrows are totally unambiguous. You never have to explain anything. And this gives you a new definition of simplicity. A simple model is one where you don't have to explain what you are doing.

Now I've cheated a little bit in this because when I talk about a calf age 0, I'm assuming that it's just been born, and I'm assuming that all calves are born at the same time of the year. That's not true of elephants. It's true of some animals that have a breeding pulse, but elephant calves can be born almost any time during the year. But for the purpose of our model, we assume that they are all born at the beginning of the year or at the beginning of our time stamp. So an elephant is unambiguously age 0, 1, 2, 3, all the way up to 59.

Well, I said that the age-structured model looks complicated, but in fact, is simple in conception. It's also simple in practice because we can reproduce that whole model with very few equations. And I'm now going to show you how we could do that.

Let's look again at our conceptual model. If you think about it, the arrow from 0 to 1 depends on the calf survival rate. The arrow from 1 to 2 depends on the adult survival rate, as does the arrow from 2 to 3, as does the arrow from 58 to 59. So in effect, all the arrows after the first arrow are the same equations, and all that's changing is whether you're going from 1 to 2 or 2 to 3 or 3 to 4. So, in effect, you have two basic equations to describe all the survival. And then, of course, you're going to have a third equation to describe the number of newborn calves. So that whole conceptual diagram can be captured, essentially, in three equations.

Well let's set out to look at what those three equations might look like. And to do that, I'm going to need to introduce some notation. First, let's have a look at a notation for parameters. We're going to need a calf survival, and I'm going to call that S subscript C. We're going to need adult survival, and that's for all survival rates other than calves, and that's S subscript A. And then we're given the calving interval, which I will call CI. And I'm going to describe the fecundity as capital F, which is just 1 upon CI. If a cow produces a calf every 3.2 or 3.3 years, then her fecundity is approximately one-third of a calf a year. Those are our parameters.

Then we're going to need some notation for our variables. And that's going to be a little bit more complicated than the notation we had in our Roc model. I'm going to use two subscripts now. I'm going to use one subscript to describe the age class and the other to describe the time stamp. So, for example, E zero T is the number of newborn female calves, emphasis on female, in year T. Then all the rest, E,KT, where K could be 1, 2, 3, all the way up to 59, is the number of females that have just turned K in year T.

And then, to simplify what we're going to write out later, I'm going to use the notation capital B subscript T for the number of breeding females in the population in year T. And that is just the sum of all the females from ages 12 through 59 in that year.

Now with those three variables, or three types of variables, and the parameters, we ought to be able to develop our equations. And I'm going to start by forgetting about the number of newborn calves in year T plus 1, and I'm going to try and calculate all the other Es at time T plus 1.

I'm going to show you the equations. I'm breaking a rule here because, remember, we learned never to write down an equation without first saying it in words. But it's so easy here that you can say it in words almost without writing it down. If I ask you the number of one-year-old calves at time T plus 1, you would say, in words, "That's the number of zero-year-old calves that survived from 0 in the time period T to T plus 1." And, obviously, that's just the survival rate SC times E-zero-T.

So, again, write it down in words, but it's pretty obvious what the answer is. The number of two year olds at time T plus 1 is the number of one year olds at time T that survived. But now the survival rate is SA, so we're going to get the equation E2T plus 1 is SAE1T. And that same argument runs through all the way to E59 T plus 1, being SA times E58 time T. See what I mean about saying that these are all, essentially, the same equation? All that's changing is 2 becomes 3 becomes 4 becomes 59, while 1 becomes 2 and becomes 58. You could do that on a spreadsheet by writing in one equation and copying it. And you're going to see how to do that in a moment.

So those are our equations for survival. We still need to calculate the number of newborn calves at time T plus 1. E-zero T plus 1. And I want to break for a second and see if you can write down the equation for E-zero T plus 1.

<u>PAUSE the video</u>: Write down the equation for the number of female calves born in t+1.

Notice that I've deliberately written down the number of female calves born in year T plus 1 because if you try to develop the equation, you're going to start with the number of breeding females at time T plus 1, which we called BT plus 1. You're going to multiply it by the fecundity, but did you remember to multiply it by one-half? And if you hadn't reminded yourself that you were talking about female calves, you would have probably forgotten to multiply by one-half. Half the calves that are born are male, and they are not appearing in our model. This just stresses, again, the importance of writing things down in words.

Well, you now have a complete set of equations for an elephant model. All you have to do is put them on a spreadsheet, and you're going to see how to do that in a moment. But before you do that, just think about what you know and don't know in this equation. You've got a reasonable value for the calving survival rate. You've got no idea of the adult survival rate, except that it'll be higher. You've got a pretty good fix on the calving interval. But your model is going to have to start somewhere. In your initial time step, you're going to have to guess at the age structure of your population, and you don't know that.

So there are two big unknowns in actually getting a spreadsheet working, and that is what initial age structure should you put in, and what's a reasonable value for the adult survival rate? Don't worry too much about that now because the heuristic we use is "press ahead regardless." These, after all, are just numbers that we're going to be able to, perhaps, guess at and try and figure out whether or not those are reasonable guesses. So we'll worry about that later.

Let's get the spreadsheet working and then see what difference they make. So over to looking at how to put this apparently-simple, but looking-rather-complicated model onto a spreadsheet.

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