Stochastic Population Growth

We’ll be studying population growth in a real population:

**MUSK OXEN**

**APPEARANCE & ADAPTATION**

MUSK OXEN are large animals with long fur coats. Both the males and females have horns. A musk oxen’s coat keeps it snug and warm. For winter they grow thick undercoats of soft brown fleece, and thick overcoats of shaggy, long straight hair that hangs down to the ground. Inuit use the soft underfur for weaving a luxurious wool.

In May they shed large amounts of fur.

**ENEMIES AND PROTECTION**

Musk oxen gather in groups of 10 to 20. They snort when annoyed. When they try to run away from enemies the musk oxen get tired and overheated. If the musk oxen sense danger they form a defensive circle around their young and face their enemies. They may even charge and try to gore the enemy with their horns. The arctic wolf is their main enemy.

**FOOD**

Musk oxen feed on grasses, lichens and willow trees. The herd keeps moving while they are eating. Their hooves spread out allowing the musk oxen to walk on snow without sinking too deep. The sharp hooves help them to get at the grasses that are buried under the snow.

**THE YOUNG**

The cows have one calf every two years. A newborn calf has a thick curly coat, but it can die from the freezing cold. It huddles under the mother’s long coat to keep warm.

**OTHER FACTS**

In the early 1900s the musk oxen were overhunted and almost disappeared. They were easy to kill when they formed a circle. Musk oxen were hunted for their meat and the hides were sold. In 1917 the Canadian government passed a law against killing the musk ox. Now there are about 60,000 musk oxen living in Nunavut.

The musk ox gives off a “muskly smell” when excited.

The family: males - bulls; females - cows; babies - calves
Our standard model of exponential population growth has been:

\[ p(1) = \text{starting population}; \ p(n+1) = rp(n), \text{ where } r \text{ represents the reproductive rate in one generation.} \]

There are many assumptions hidden in this model. The first is that an entire population can be modeled by what the behaviour of some sort of average -- which is what \( r \) is. Yet we know that in real life, some oxen will be standing on ice just when it decides to break away, and those oxen will float away, never again to contribute to the population of their herd. Others will fall ill for a year and be unable to reproduce.

The variation between individuals, and the contribution of this to variation in the size of the herd, has the technical name: \textit{demographic stochasticity}.

\textbf{stochastic, a.}

[ad. Gr. \\textit{stochastikè}, f. \\textit{stochástēs} to aim at a mark, guess, f. \\textit{stóχε} aim, guess.]

1. Pertaining to conjecture. Now rare or Obs.

\textit{1662} J. OWEN Animad. on Fiat Lux Pref. 4 But yet there wanted not some beams of light to guide men in the exercise of their Stocastick [sic] faculty. 17. J. WHITEFOOT in Sir T. Browne's Wks. (1712) I. p. xxxvii, Tho' he [Browne] were no Prophet...yet in that Faculty which comes nearest it, he excelled, \textit{i.e.} the Stochastick, wherein he was seldom mistaken, as to future Events. 1720 SWIFT

What does this mean, in muskox terms? Here’s David Quammen, in his book, Song of the Dodo:

“In general, there are four sources of uncertainty to which a population may be subject,” Shaffer wrote. He listed them: demographic stochasticity, environmental stochasticity, natural catastrophes, genetic stochasticity. Behind the jawbreaker terminology were some easily digestible ideas.

Demographic stochasticity means accidental variations in birth rate, death rate, and the ratio of the sexes. Say you have an extremely rare species—make it another hypothetical beast, call it the whitefooted ferret. Only three individuals survive, a female and two males. The female breeds with one male, gives birth to a litter of five, then dies. By an unfortunate chance, the newborn ferrets are all males. Demographic stochasticity. Now you have seven white-footed ferrets but no females, and extinction is inevitable.

Environmental stochasticity means fluctuations in weather, in food supply, and in the population levels of predators, competitors, parasites, and disease organisms with which your jeopardized species must cope. Say you have eighteen white-footed ferrets, with a balanced sex ratio, but the prairie dog colony on which they depend for food and shelter is being killed off by a virus. Your ferrets are not susceptible to the virus. Still, without enough prairie dogs to eat, they begin starving. They die back to a mere handful. A three-year drought makes their lives miserable, each long dusty summer adding stress to their situation; then comes a ferociously hard winter. Environmental stochasticity. Hungry, inadequately sheltered, the ferrets go extinct.
In this set of problems, instead of watching the average behaviour of our musk-ox herd, we’re going to follow each individual through a full year. At the end of the year we’ll count up how many oxen we have.

Muskox once roamed the entire Arctic slope of Alaska but were either never abundant or were diminishing in abundance before the advent of firearms. Last known animals were killed near Barrow around 1850-60 (Hone 1934, Bee and Hall 1956) Interest in re-establishing muskox on former Alaskan range stimulated a memorial to Congress by the Legislature of the Territory of Alaska in 1927 urging the appropriation of funds for this purpose. A sum of $40,000 was authorized in 1930 to secure stock from Greenland. In anticipation of the requirement for a location to develop the introduced herd, Nunivak Island was designated as a National Wildlife Refuge for use “in contemplated experiments in re-establishing the muskox as a native animal in Alaska” (U.S. Gov’t. Executive Order 5095, April 1929). Although Nunivak Island was quite different from the Alaskan Arctic Slope or the muskox ranges in Canada and Greenland, there were certain advantages that determined the selection of the island as a range for the nucleus herd. Nunivak was relatively accessible, was free from predators, and permitted confinement on a large area of apparently good habitat. None of these requirements could have been met in the Arctic. In retrospect, the choice was most appropriate. During the summer of 1930, a total of 34 animals including 8 male and 9 female calves, 7 male and 9 female yearlings, and 1 sub-adult female was captured in Greenland. These were landed in New York on September 15, held in quarantine there until October 18, and then shipped to Alaska, arriving at College on November 5. (No animals were lost in transit (Palmer 1938). All animals were held in a wooded pasture at the University of Alaska until they were released on Nunivak in 1935 and 1936. At least 19 calves were born at the University, but predation by black bears (Etiarctos americanus) and various other losses reduced the herd to 31 animals prior to release. (from Spencer, D and Lensink, C, The Muskox of Nunival Island, Alaska, Journal of Wildlife Management, 1970, 34 pps 1-15.)
We’ll start our work with \( P(0) = 31 \) animals, as above. The average survival rate was measured as \( .921 \). One way to implement this is the following: for each of the 31 animals, choose a random number (make sure it is \textit{uniformly distributed}) between zero and one. If that number is less than or equal to \( .921 \), the animal survives into the next year. Otherwise, it dies.

Now, each animal that survives has a \( .277 \) chance of begetting one more animal. Again, we can use a random number generator to simulate that, animal by animal. At the end, we have the number of animals left, after one year.

1) Program and run the above simulation 1,000 times. For each run \( k \), save the number \( n(k) = \) the population you get. Then plot a histogram of the values you get.

2) Now change the histogram to a cumulative population distribution. That is, let \( d(j) \) represent the fraction of times that the population had value less than or equal to \( j \). (“fraction of” here means, total number of times, divided by 1,000). You should get an S-shaped curve.

3) From your histogram: what is the most likely population size?

4) Knowing that the survival rate is \( .921 \) and the birth rate \( .277 \), what would the Malthusian model predict as the population after a year? From your graph: what is the probability the population will be less than the Malthusian prediction by as much as \( \pm 20\% \)? What is the probability that the population will be greater than that predicted by the Malthusian model, by as much as \( \pm 20\% \)?

5) If the population drops below four individuals, it is likely to go extinct. What is the probability of this happening?

6) Rerun the simulation 5,000 times and 10,000 times. By what percentage do the quantities in problem 4 change? Graph all three cumulative population distributions on the same graph. What do you conclude?

Even this model makes assumptions, for example that growth rates are constant over the several years. But some years will be cold and there won’t be enough food; newborns will starve or cows will be unable to conceive. As stated in \textit{Role of Landscape Use in the Regulation of Large Herbivore Populations}, “For muskoxen, the proximate control over reproduction is the quality of late summer-autumn range (i.e., during the rutting season), specifically, the food resource that controls the acquisition of body reserves supporting gestation. When these reserves are insufficient, female muskoxen fail to conceive and undergo a breeding pause”. Factors such as these are referred to as \textit{environmental stochasticity}, and they act on the population as a whole, affecting the reproductive rate \( r \). To model this, we’d write

\[
p(1) = \text{starting population}; \quad p(n+1) = (\text{random})p(n)
\]

7) Here ‘\textit{random}’ is a random number that is different for each generation \( n \). We wouldn’t expect ‘\textit{random}’ to be uniformly distributed. But what kind of distribution should ‘\textit{random}’ have? One way to answer this is to use real data of what kinds of \( r \)’s occurred historically. This data is contained in the Spencer and Lensink article, referenced above. Use the population data from 1936 to 1964 to estimate the growth rate from year to year. now make a histogram of the growth rates; the bin size should be about \( .025 \)

8) Model population growth of musk oxen over 20 years, each year using a growth rate drawn randomly, with a frequency distribution as in the histogram of #7. Run this 1,000 times. Once again, For each run \( k \), save the number \( n(k) = \) the population you get. Then plot a histogram of the values you get, and compute the cumulative frequency distribution. Answer the same questions as in problems #4 and #5 above.