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A statistical investigation into the properties and dynamics of biological populations experiencing environmental variability

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2007-02-15T11:30:22Z
http://hdl.handle.net/10539/2003

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Chapter 1: Introduction

This research report is primarily a synthesis of some of the more common approaches to population modelling. The report focuses on stochastic population modelling; specifically on models that account for environmental variability. This emphasis is justified by the environment's considerable sway over a population's wellbeing. The ultimate aim is to create a model that is both a dynamic and an accurate representation of a population within a varying environment.

Population models enable us to explore the dynamics of population behaviour. Such an understanding serves more than a theoretical purpose: it allows us to predict the response of the model to predetermined exogenous conditions. These models are a useful tool for inference; enabling one to derive a range of properties about a population and its drivers. It thus follows that population models can help to advance the knowledge of various biological systems and their functions as well as being important at the planning stage in practical areas like conservation and pest control.

A cursory examination of population data for any individual species should elucidate the considerable changes that a population may undergo over time. Apart from the immediate randomness that one may perceive in the data, there is often a series of patterns or trends present that hint at an underlying data structure. These "deterministic components" are often indicative of some fundamental characteristic or property of the population or, alternatively, of the population's interaction with the environment and other species. Both the random and the deterministic components need to be conceptualized if an accurate representation of the population is to be attained.

Biological populations are subject to significant stochastic variations. Rand and Wilson (1991) partitioned these stochastic effects into three classes:

i. demographic fluctuations arising from the stochastic nature of the population
ii. randomness in the environment (i.e. exogenous fluctuations), and thereby in the parameters affecting the population
iii. measurement errors

The relative magnitudes of the first two types of random fluctuations (and a population's response to them) will play an essential part in determining the viability of the population in the future.

A population often has a predictable response to external driving factors. The population's response provides insight into the mechanics of the interaction between a population and its drivers – it also reveals something of the very nature of the population. The exogenous factors driving a population include:

i. the surroundings in which a population lives (e.g. rainfall, geographical features)
ii. the population numbers of competing species
iii. the population numbers of plant, predator and prey species
iv. random events, both on a small and a large scale
v. physical condition of each member of the population

By allowing for the various drivers, an accurate population model can be built. We will now look at the basic building blocks of a population model.

All the approaches to population modelling that are covered within this research report (with the exception of branching processes) are based on the concept of the transition rate. The population transition rates are the (possibly time inhomogeneous) rates at which each of four basic processes act on the population – any population consisting of a fixed number of individuals, N, can only change due to birth, death, immigration or emigration. Thus, by examining the rates at which each of these four events occurs, one can account for all the possible variations that take place.

Let B, D, I and E be the rates at which births, deaths, immigration and emigration occur. Thus:

- P[birth occurs between t and $t+\Delta t$] = $B\Delta t + o(\Delta t)$
- P[death occurs between t and $t+\Delta t$] = $D\Delta t + o(\Delta t)$
- P[immigration occurs between t and $t+\Delta t$] = $I\Delta t + o(\Delta t)$
- P[emigration occurs between t and $t+\Delta t$] = $E\Delta t + o(\Delta t)$

Consequently, in a small interval, Δt, the corresponding change in the population, ΔN, is given by $\Delta N = (B - D + I - E)\Delta t + o(\Delta t)$ where $\lim_{\Delta t \to 0}\left(\frac{o(\Delta t)}{\Delta t}\right) = 0$. A significant proportion of the models to be covered assume that birth and death are the only two processes that act on a population i.e. they ignore migration. So by focusing on these two processes, one can create an archetypal model of the population numbers.

At this stage, it might be helpful to look at some raw wildlife data so as to get a feel of population numbers and their trajectories. The following data was collected from the

Kruger National Park by way of an aerial census. (Special thanks to Prof. Norman Owen-Smith, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand.) Data was obtained between 1980 and 1993 and is a record of the change in eland population numbers from year to year. Unfortunately, the data contains significant measurement errors – eland are difficult to observe against a backdrop of dry, brown grass, which often leads to a sizeable undercount in dry seasons. This could lead to large distortions of the trends in the eland population numbers. (For a means to deal with uncorrelated measurement errors, refer to Chapter 7.)

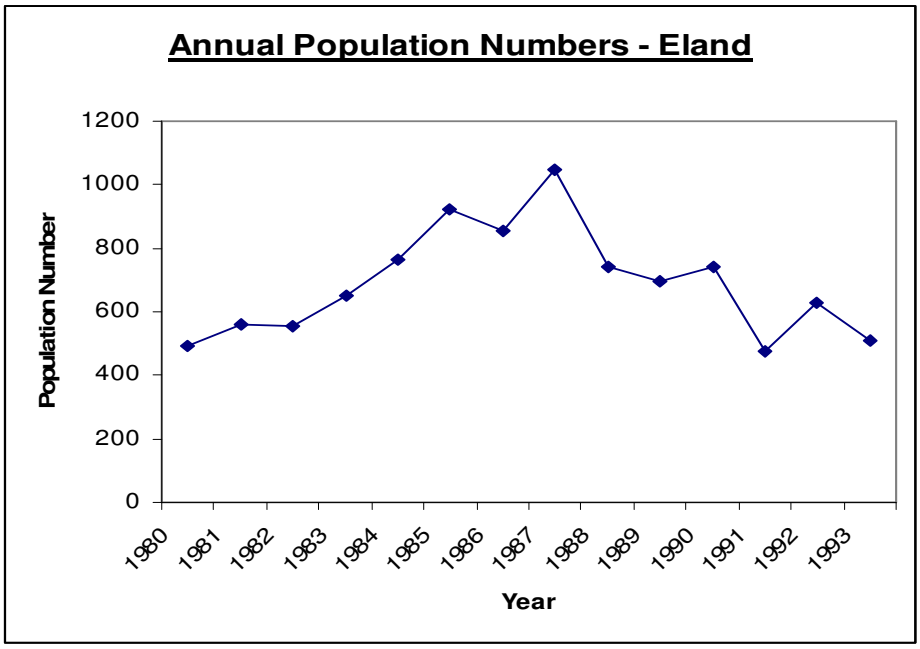


Figure 1.1 Eland population numbers in the Kruger National Park

The eland population appears to have peaked in 1988, followed by a period of sustained decline. Over the latter period, the population numbers appear to be shifting more erratically. However, this could be as a result of measurement errors rather than any fundamental changes in the population. In the above example, the objective of population modelling will be to try and understand the forces (e.g. predation, rainfall, disease) that may have caused the above population trajectory.

The mathematical models covered within this research report can be divided into two broad sections: models that ignore environmental variability and models that incorporate environmental variability. Chapter 2 gives brief treatments of a number of deterministic models. Chapters 3 and 4 describe the traditional approaches to population modelling. In Chapter 5, various models that include the environment are covered whilst Chapter 6

investigates the affect of extreme environmental changes on the population. Chapter 7 explores the likelihood approach of estimating parameters for a population model. Finally, Chapter 8 gives a brief overview of all the concepts that were covered in this research report.

Simulations are performed frequently in Chapters 3 – 7. The number of simulations performed varies. In most cases, the number of simulations executed was set so as to take roughly an hour of computing time – though in Chapter 6 simulations took roughly 8 hours to run! (The simulations were executed in Microsoft Excel on a Pentium 4, 2800MHz, 512MB RAM.) In all cases, this resulted in at least ten thousand simulations being performed. This should thus ensure that any inferences based on the simulations should be reliable.