A GENERALISED VERHULST MODEL WITH IMPLICATIONS FOR OPTIMAL SEASONAL CONCEPTION STRATEGIES.

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Abstract. A generalised Verhulst model subject to seasonal change in both growth rate and carrying capacity is outlined. Numerical solutions to the Verhulst equations are employed to obtain optimal growth rate phase shift with respect to carrying capacity. Possible genetic drift in preferred seasonal conception strategies are investigated using agent based simulations.

Introduction

In 1842 Alfred Lord Tennyson wrote the poem *Locksley Hall* [5] in which appears the immortal line:

> *In the Spring a young man's fancy lightly turns to thoughts of love*

A 50 year study of a conservative scottish population in the first half of the 20th century undertaken by Russell et al [2] shows sinusoidal trends in birth rate data that both confirms the poet's claim and provides evidence for environmental driven birth cycle. We quote from that paper:

> *Examination of the birth rhythm found in different parts of the world show either one or (more frequently) two peaks. The classic European pattern is one with a main peak in spring (summer conceptions) and a smaller one in the autumn (winter conceptions).*

In this article we will use a modified Verhulst model to show that the timing of conceptions by a population governed by a seasonal carrying capacity has a marked effect on the resilience of the population as a whole. We then make use of an agent based simulation to demonstrate that seasonal carrying capacity might be responsible for a genetic drift in a human population that favors a predisposition to winter conceptions. Both the Verhulst model and the agent based simulation are implemented with R scripts that make use of a open source R package `simecol` [4].

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A generalised Verhulst Model

The standard Verhulst model of population growth, given by

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t)}{k}\right) \tag{1}$$

where r is the per capita intrinsic growth rate and k is the carrying capacity of the habitat. It is well known that if $N(0) < k$, then $N(t)$ tends monotonically to k. See [1] for an analysis of standard Verhulst models.

The above result will be true even if r is a function of time provided k is constant. However, the result may not be true if k is also a function of time. In [3] we point out that in this case the model demands that $N(t)$ will increase if at some time t both $N(t) > k(t)$ and $r(t) < 0$ which is clearly counter productive. This observation led us to propose a modified Verhulst model:

$$\frac{dN}{dt} = \left\{ \begin{array}{ccc} r(t)N(t)\left(1 - \left(\frac{N(t)}{k(t)}\right)\right) & \text{for} & N(t) \le k(t) \\ -\left|r(t)N(t)\left(1 - \left(\frac{N(t)}{k(t)}\right)\right)\right| & \text{for} & N(t) > k(t) \end{array} \right\} \tag{2}$$

We illustrate the modification using sinusoidals to model seasonal fluctuations in carrying capacity and growth rate. The growth rate has the same period as the carrying capacity but is phase shifted by a user specified parameter, ϕ.

$$\begin{array}{rcl} k(t) & = & B - C\cos(2\pi t) \\ r(t) & = & A\cos(2\pi(t+\phi)) \end{array} \tag{3}$$

In Figure 1, we demonstrate the effect of phase shift in seasonal birth rate. In each frame we compute two solutions to the Verhulst model, one in which the initial population is below the carrying capacity and the other in which the initial population is above the carrying capacity. In top frame the phase shift in the growth rate is set to $\phi = \frac{1}{2}$ and both solutions to the modified model eventually become periodic and oscilate just below the mean carrying capacity. In the bottom frame the phase shift in growth rate is set to $\phi = 1$ and we observe that this is detrimental to population's survival in the long run as both solutions now drop well below the mean carrying capacity.

Numerical experiments show that the plots given in Figure 1 depict the two extremes in the effect of the phase shift parameter. R scripts for reproducing these

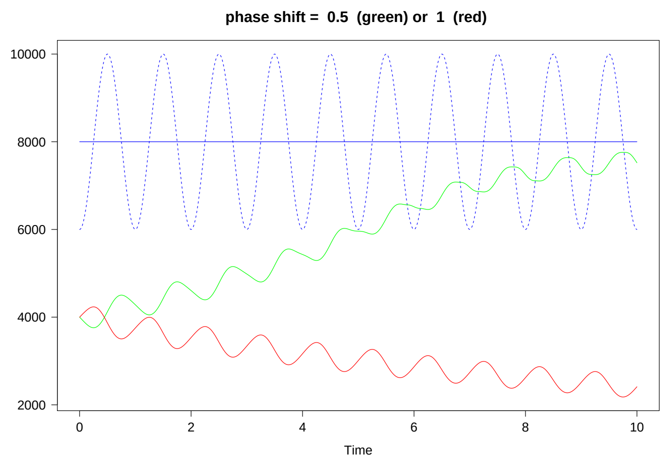

FIGURE 1. Solutions to the modified Verhulst model, $A = 1, B = 8000, C = 2000$ and $\phi = \frac{1}{2}$ (left) or $\phi = 1$ (right)

plots are given in the appendix. A phase shift of $\phi = \frac{1}{2}$ is the best possible strategy for a population trying to recover it's habitat's carrying capacity after a natural disaster.

In Figure 2 we magnify the first year of the population's evolution to see that the best strategy for a recovering population is to time the maximum growth rate to coincide with the peak of the carrying capacity whilst the worst strategy is if the most negative growth rate coincides with maximum carrying capacity.

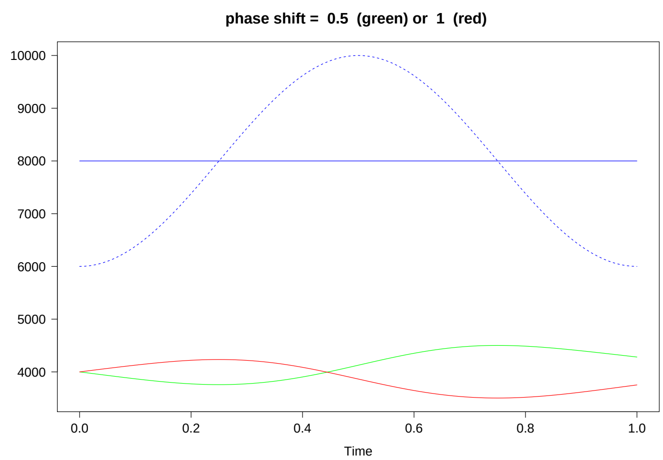

FIGURE 2. Magnified solutions to the modified Verhulst model, $A = 1, B = 8000, C = 2000$ and $\phi = \frac{1}{2}$ (left) or $\phi = 1$ (right)

In the next section we investigate whether this *law of nature* could result in a genetic drift to a preferred season of conception.

An agent based simulation

We will now employ the same R package, `simecol` [4], to construct an agent based simulation of a maternal population of individuals evolving under the influence of a seasonal carrying capacity.

Each individual in our simulation will be female with 3 state variables:

`age`	the current age (in months) of this individual
`cpm`	the preferred conception month of this individual
`fetus`	the current age (in months) of this individual's fetus

The age distribution of the initial population is biased towards young individuals by means of a beta distribution. Initially preferred conception months for each individual are distributed uniformly over the whole year and no fetuses are present.

The population then undergoes monthly updates:

- `live:` Each individual and each fetus in the population has their age incremented by one month.
- `survive:` Using our seasonal carrying capacity and a mortality model due to xxxx [**?**] individuals are selected for termination and removed from the population
- `birth:` Fetuses reaching 9 months in age are upgraded to fully fledged individuals and inherit their preferred conception month from their mothers. This inheritance may undergo some drift.
- `conceive:` Individuals in the appropriate age bracket that do not currently possess a fetus and who's preferred conception month is this month are randomly selected for child bearing.

The `simecol` package allows us to evolve the population over time keeping track population size and distribution of preferred conception month. In Figure 3 we show the results of a 250 year long simulation. The population converges on the mean carrying capacity and the preferred conception month drifts towards October.

In Figure 4 we give snapshots of the drift in the distribution of preferred conception month over the running time of the simulation.

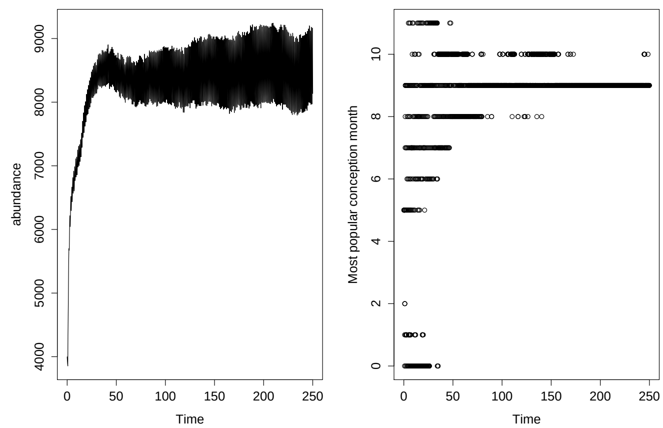

FIGURE 3. Output from the agent based model, $N(0) = 10000, k(t) = 8000 + 2000\cos(t)$

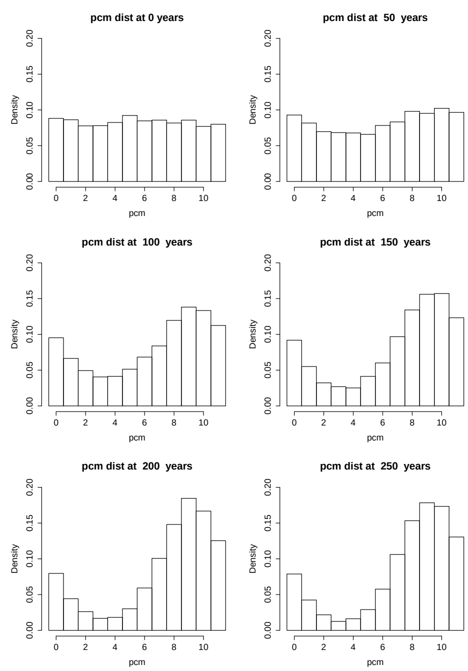

FIGURE 4. Output from the agent based model, $N(0) = 10000, k(t) = 8000 + 2000\cos(t)$

Acknowledgements

John Henry Swart, Emeritus Professor and former Head of Mathematics, passed away at his Westville home on 21 July 2012. He is survived by his wife Henda (also

an Emeritus Professor of Mathematics at UKZN) and their children Christine, Sandra and Gustav.

John Swart was born on 11 February 1940 in Kimberley. He grew up in Williston. His undergraduate studies and MSc were completed at Stellenbosch University. In 1969 he obtained his PhD under the supervision of Professor Hanno Rund (who was based at UNISA at that time).

John's lifelong and infectious enthusiasm for mathematics influenced the community in which he lived and worked for many decades. His research concerned partial differential equations and biological mathematics. He was an active member of the South African Mathematical Society and served on its executive. He took an interest in local secondary schooling as well, delivering multiple talks at schools and meetings of mathematics teachers.

John's association with UKZN began when he was appointed as a lecturer at the former University of Durban-Westville in 1962. He took up a position at the former University of Natal (Durban) in 1965, where he served as Head of the Department of Mathematics and Applied Mathematics from 1980 to 1985. He served two further terms as Head of the School of Mathematical Sciences, from 1993 to 2000. He gave very extensive service to the university through the Boards of Science and Engineering, as well as Senate, Council and countless university committees, culminating in a term as Pro-Vice Chancellor. He retired from UKZN in 2005.

John's vast experience, his forthright and articulate persona, and the breadth of his involvement in university affairs make him an unforgettable figure in the institution's history. As such he will be remembered fondly by colleagues young and old, and by generations of science and engineering students.

Conclusion

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