Harvesting the Single Species Gompertz Population Model in a Slowly Varying Environment

Stuart Roberts

Supervised by John Shepherd

RMIT

Postal Address: 111 Barry Street
c/- The University of Melbourne
Victoria 3010 Australia

Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 9349 4106
Web: www.amsi.org.au

Introduction

The single species Gompertz population model was first proposed by Benjamin Gompertz in 1825 [1] as a model for the growth of human populations.

$$\frac{dP}{dT} = RP\log\left(\frac{K}{P}\right), \qquad P(0) = P_0\,, \tag{1}$$

where P is defined to be the population, T is the time parameter, R is the population growth rate, K is the carrying capacity of the environment and P_0 is the initial population.

In 1964, Laird [2] successfully used the Gompertz model to model the growth of tumour cells in a confined space. It can be argued that the treatment of tumour growth by chemical means could be modelled by a harvested Gompertz equation with density dependent harvesting, giving the model

$$\frac{dP}{dT} = RP\log\left(\frac{K}{P}\right) - EP, \qquad P(0) = P_0\,, \tag{2}$$

where E is a positive constant. We will investigate the effect of this harvesting term E on the model and how large this value must be for the population to be driven to zero in infinite time. We can also determine the time taken to drive the population below a given proportion of the initial population for a given E.

We will extend this investigation to the case where all the model parameters (R, K and E) vary slowly with time. Such systems can be approximated using numerical methods, though these methods do not provide a detailed insight to the trends of the model. Instead, this will be modelled using a multitiming technique, in order to investigate the effect of the model parameters on the trends of the system.

Comparison of the Gompertz Model to the Harvested Gompertz Model

The harvested Gompertz model (2) is a separable DE and can be solved exactly. The harvested population as a function of time is given by

$$P(T) = K\exp\left(\frac{\beta\exp(-RT) - E}{R}\right), \tag{3}$$

where

$$\beta = R\log\left(\frac{P_0}{K}\right) + E. \tag{4}$$

By setting E to zero, the solution (3) reduces to that for the unharvested model (1) as expected. Interestingly, regardless of the size of E, the population can never be driven to zero in infinite time. Instead as $T \to \infty$, we observe $P(T) \to K\exp\left(-\frac{E}{R}\right)$. The limit is expressed in terms of the carrying capacity and a ratio between the harvesting coefficient and growth rate. In the case of modelling the treatment of tumour cells, this limiting state is not a problem, since the number of tumour cells will be discrete, so the limiting value can be driven close enough to zero for all cells to be killed.

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia
Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

Setting $E = 0$ in (3), the limit of the unharvested model is $P(T) \to K$, the carrying capacity, as $T \to \infty$. Given the restriction that $E > 0$ the limiting state of the harvested model will always be less than the limit of the unharvested model.

Figure 1 shows the decline in the limiting state as we increase the value of *E* for fixed values *K, R* and P_0. The model is strictly increasing or decreasing, depending on where the initial population is in comparison to the limiting state.

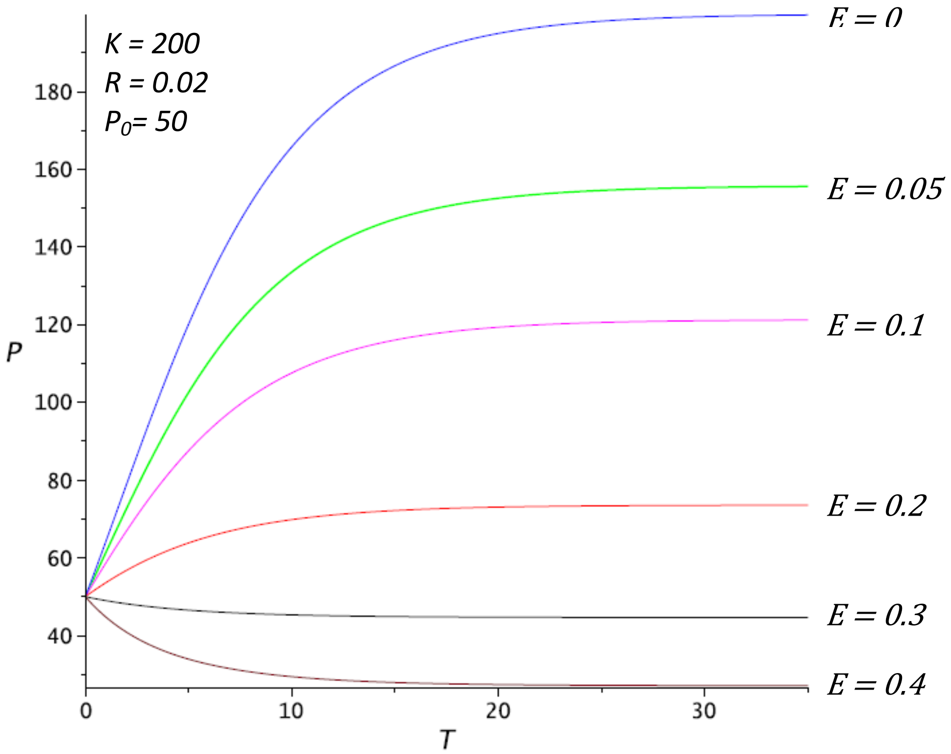

Figure 1: Plot of the unharvested Gompertz model (E=0) to five harvested models with K=200, R = 0.02 and P_0=50.

Reduction to a Portion given *E* or *T*

If we have an understanding of what factors affect the value of *E* in the model, we may determine the time needed to reduce the population to a prescribed value. If we express this value as a proportion of the initial population P_0, we can get an expression (at least in the constant coefficient case) for the amount of time to pass before the population is driven below some value.

Let $\hat{P}$ denote the fraction of the initial population we wish to drive the population to. We want to solve for *T* such that

$$P(T) = K \exp\left(\frac{\beta \exp(-RT) - E}{R}\right) \leq \hat{P} P_0 . \qquad (5)$$

By rearranging this inequality we can find the expression for the time that must have passed to reach the desired population, as

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia
Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

$$T \geq -\frac{1}{R}\log\left\{1+\frac{R\log(\hat{P})}{E+R\log\left(\frac{P_0}{K}\right)}\right\}. \qquad (6)$$

Similarly, we can find the desired value of *E* required to reduce the population below a given proportion in time *T.* By rearranging (5) we get

$$E \geq R\left\{\frac{\log(\hat{P})}{\exp(-\mathrm{RT})-1}-\log\left(\frac{P_0}{K}\right)\right\}. \qquad (7)$$

Both equations (6) and (7) are valid only if both the initial population and desired population are both greater than the limiting value. That is $K\exp\left(-\frac{E}{R}\right) < \hat{P}P_0$ where $0 < \hat{P} < 1$. For a varying environment these inequalities may not hold, since there is no guarantee that the varying parameters will not bring the population back above the desired level.

A Slowly Varying Environment

It is often problematic to describe the growth of populations in terms of constant coefficients, since environments are rarely constant. Changes in the weather, the introduction of new species and disease have an effect on the population parameters. The effect of some of these factors may sometimes be subtle, but it is important to incorporate them into the model. In the case of treating tumours, the intensity of the chemical treatment may change the value of the harvesting parameter over time. We will look into the case that all coefficients of the system vary with time.

Multi-Scale Model

We first want to rewrite the model (2) in terms of non-dimensional parameters. For the constant coefficient case at least, this simplifies the problem and may highlight values that are better measured relative to one another. The limit of the system being dependant on the ratio between the harvesting coefficient and growth rate is one example. The non-dimensional time and population variables will be defined by;

$$t = R_0 T\,, \qquad (8)$$

$$p(t) = \frac{P(T)}{K_0}\,, \qquad (9)$$

where *t* and *p* are the non-dimensional time and population parameters respectively. The new forms of the existing parameters will be written in the form;

$$R(T) = R_0 r\left(\frac{T}{T_R}\right), \qquad (10)$$

$$K(T) = K_0 k\left(\frac{T}{T_K}\right), \qquad (11)$$

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia
Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

$$E(T) = E_0 e\left(\frac{T}{T_E}\right), \tag{12}$$

where *r, k* and *e* are dimensionless functions that vary with time. Note that in the case of constant coefficients, *r, k* and *e* are equal to 1. R_0, K_0 and E_0 are characteristic values of the parameters and T_R, T_K and T_E are characteristic time scales. In order for these functions to be slowly varying the ratio of the population time scale to the characteristic time scales must be small. We define a small value;

$$\varepsilon = \frac{1}{R_0 T_R} = \frac{1}{R_0 T_K} = \frac{1}{R_0 T_E}\,. \tag{13}$$

This gives the non-dimensional form of the model (2), as

$$\frac{dp(t)}{dt} = r(\varepsilon t)p(t)\log\left(\frac{k(\varepsilon t)}{p(t)}\right) - \lambda e(\varepsilon t)p(t), \qquad p(0) = \frac{P_0}{K_0} = \mu\,, \tag{14}$$

where $\lambda = E_0/R_0$. This model can now be seen to vary on two different time scales; the population time scale *t* and the slowly varying larger time scale εt. We will attempt to express the solution to this problem as a function of these two time scales, as well as a function of the time-scaling constant ε. To avoid complications, a more general time scale needs to be proposed [3],

$$t_0 = \frac{1}{\varepsilon} g(t_1) \;\text{ and }\; t_1 = \varepsilon t\,. \tag{15}$$

The population function can be now be expressed as a function of t_0 and t_1 as

$$p(t) \equiv \tilde{p}(t_0, t_1, \varepsilon)\,. \tag{16}$$

The chain rule needs to be applied to get an expression for the derivative of this new function. Applying this rule gives

$$\frac{dp(t)}{dt} = g'(t_1)D_0\tilde{p} + \varepsilon D_1\tilde{p}\,, \tag{17}$$

where D_0 and D_1 are partial differential operators with respect to t_0 and t_1 respectively. After these transformations we have the partial differential equation

$$g'(t_1)D_0\tilde{p} + \varepsilon D_1\tilde{p} = r(t_1)\tilde{p}\log\left(\frac{k(t_1)}{\tilde{p}}\right) - \lambda e(t_1)\tilde{p}\,. \tag{18}$$

This form allows a perturbation approach to be used, since ε is now expressed explicitly.

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia

Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

Perturbation Approach

For the perturbation approach we express $\tilde{p}$ as a perturbation expansion in ε.

$$\tilde{p}(t_0,t_1,\varepsilon)=\tilde{p}_0(t_0,t_1)+\varepsilon\tilde{p}_1(t_0,t_1)+\varepsilon^2\tilde{p}(t_0,t_1)+O(\varepsilon^3)\,. \tag{19}$$

Substituting this expansion into (18) and collecting like powers of ε we get equations to solve for $\tilde{p}_0$ and $\tilde{p}_1$ as

$$g'(t_1)D_0\tilde{p}_0=r(t_1)\tilde{p}_0\log\big(k(t_1)\big)-r(t_1)\tilde{p}_0\log(\tilde{p}_0)-\lambda e(t_1)\tilde{p}_0 \tag{20}$$

and

$$\begin{aligned} g'(t_1)D_0\tilde{p}_1+\ & D_1\tilde{p}_0 \\ &=r(t_1)\tilde{p}_1\log\big(k(t_1)\big)-r(t_1)\tilde{p}_1\log(\tilde{p}_0)-r(t_1)\tilde{p}_1-\lambda e(t_1)\tilde{p}_1\,. \end{aligned} \tag{21}$$

Solving equation (20) we find

$$\tilde{p}_0=k(t_1)\exp\left\{B(t_1)\exp\left(\frac{-r(t_1)}{g'(t_1)}t_0\right)-\frac{\lambda e(t_1)}{r(t_1)}\right\}. \tag{22}$$

where $B(t_1)$ is an arbitrary function of t_1. It is important for $B(t_1)$ to be bounded in order for (22) to satisfy the original limit $K\exp(-E/R)$ as $t\to\infty$ for the constant coefficient case. Expression (22) can now be substituted into (21) in order to find a particular solution for $\tilde{p}_1$ given by

$$\begin{aligned}\tilde{p}_1=\frac{-\tilde{p}_0}{g'(t_1)}&\left\{\frac{k'(t_1)g'(t_1)}{k(t_1)r(t_1)}+B'(t_1)t_0\exp\left(-\frac{r(t_1)t_0}{g'(t_1)}\right)\right.\\ &\left.-\frac{B(t_1)}{2}\left(\frac{r(t_1)}{g'(t_1)}\right)'t_0^2\exp\left(-\frac{r(t_1)t_0}{g'(t_1)}\right)-\frac{g'(t_1)}{r(t_1)}\left(\frac{\lambda e(t_1)}{r(t_1)}\right)'\right\}.\end{aligned} \tag{23}$$

In equation (22), as $t_0\to\infty$, $\tilde{p}_0$ tends to the slowly varying limiting state $k(t_1)\exp(-\lambda e(t\_1\,)/r(t\_1\,)\,)$. This has an exponential rate of convergence. So we expect the rate of convergence of $\tilde{p}_1$ to be exponential also. To achieve this, the terms $t_0\exp(\dots)$ and $t_0^2\exp(\dots)$ must be excluded. We will set the values of these coefficients to zero, giving

$$B'(t_1)=0\Rightarrow B(t_1)=C_1\,, \tag{24}$$

where C_1 is an arbitrary constant. We also need to set

$$\left(\frac{r(t_1)}{g'(t_1)}\right)'=0\ \Rightarrow\ r(\mathrm{t}_1)=g'(t_1)\,. \tag{25}$$

We can now express t_0 in terms of known functions. Equation (15) and (25) imply

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia
Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

$$t_0 = \frac{1}{\varepsilon}\int_0^{t_1} r(s)ds. \tag{26}$$

Together with the initial conditions we can solve for $\tilde{p}_0$ and $\tilde{p}_1$, to obtain a two term expansion (19) for the evolving population $\tilde{p}$.

$$\begin{aligned}\tilde{p}(t_0, t_1, \varepsilon) = k \exp\left(c_0 \exp(-t_0) - \frac{\lambda e}{r}\right) \\ + \varepsilon\Bigg\{kc_1 \exp\left(c_0 \exp(-t_0) - \frac{\lambda e}{r} - t_0\right) \\ + \frac{k}{r}\left(\lambda\left(\frac{e}{r}\right)' - \frac{k'}{k}\right)\exp\left(c_0\exp(-t_0) - \frac{\lambda e}{r}\right)\Bigg\} + O(\varepsilon^2)\end{aligned} \tag{27}$$

where,

$$c_1 = \frac{-1}{r(0)}\left(\lambda\left(\frac{e(t_1)}{r(t_1)}\right)'\Big|_{t_1=0} - \frac{k'(0)}{k(0)}\right) \tag{28}$$

and

$$c_0 = \log\left(\frac{\mu}{k(0)}\right) + \frac{\lambda e(0)}{r(0)}. \tag{29}$$

Expression (27) gives an approximation to the solution of problem (14) when the model has slowly varying coefficients. Substituting $E_0 = 0$ into the above equation, we can also get an approximation for the unharvested model varying in a slow environment. This substitution agrees with prior work by Grozdanovski [3], which has been done on the unharvested model in a slowly varying environment.

In (27) as $t_0 \to \infty$ we observe a slowly varying limiting state given by

$$\lim_{t_0\to\infty} \tilde{p} = k\exp\left(-\frac{\lambda e}{r}\right) + \frac{\varepsilon k}{r}\left\{\lambda\left(\frac{e}{r}\right)' - \frac{k'}{k}\right\}\exp\left(-\frac{\lambda e}{r}\right). \tag{30}$$

This limit is the sum of two terms. The first term is the same as the original limiting state, and the second term is expressed in terms of derivatives of the slowly varying parameters. This term should be small for significantly small ε.

Since the second term of (30) is expressed in terms of derivatives of the slowly varying parameters, in the case where we have constant parameters ($e = r = k = 1$), this limiting state reduces to

$$\lim_{t_0\to\infty} \tilde{p} = k\exp(-\lambda)\,. \tag{31}$$

After transforming back to the original parameters in (2) we find

$$\lim_{T\to\infty} P = K\exp\left(-\frac{E}{R}\right). \tag{32}$$

This limit is the same as the original problem, implying our expansion is consistent with the constant parameter case.

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia

Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

Comparison to Numerical Solutions

To test the accuracy of the approximation, we can compare our solutions with solutions found using numerical methods. Figure 2 shows a plot of the multitime approximation along with the solution using the Runge-Kutta method in Maple for $\varepsilon = 0.05$, where both the harvesting parameter and carrying capacity vary slowly with time. For these particular parameters, we can see that the approximation is very close to the numerical solution over the entire domain. For cases when $\varepsilon = 0.05$, we observed similar accuracy for other choices of e, k and r.

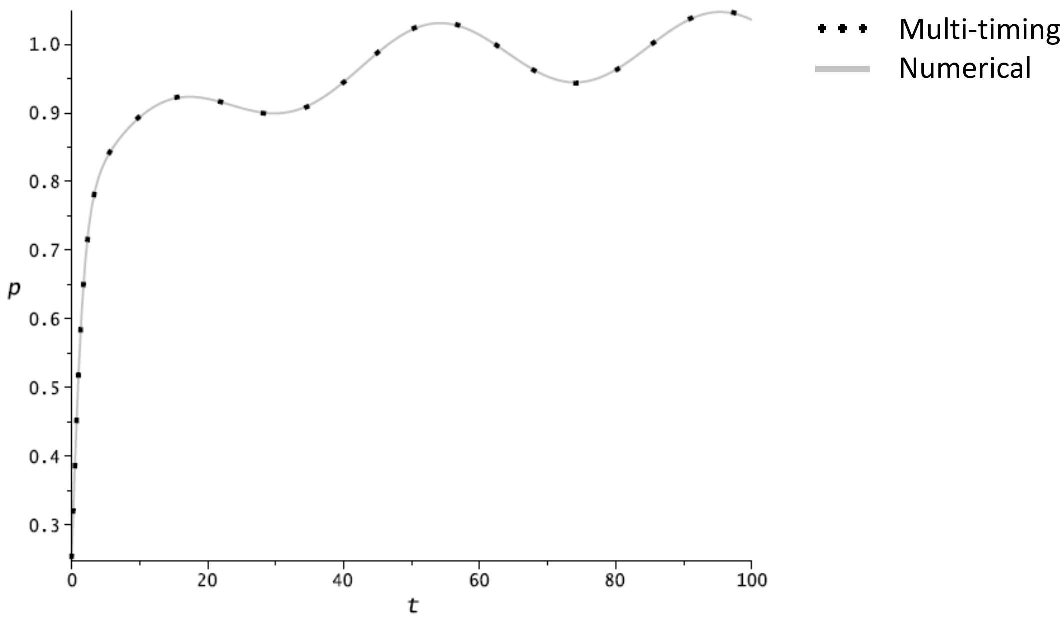

Figure 2: Plot of the multitime approximation against numerical solution for $\varepsilon = 0.05$ varying harvesting parameter ($e = \exp(-t_1)$) and carrying capacity ($k = 1 + 0.05\sin(3t_1)$)

However, as we increase the value of ε the multitime method begins to fail. In figure 3 we can see that the error of the approximation becomes more obvious as it deviates from the numerical solution. This is due to the error term $O(\varepsilon^2)$ becoming more significant for larger ε. Typically the errors became obvious around $\varepsilon = 0.1$- 0.15. This problem could be overcome by increasing the expansion to the second power of ε, though seemingly unnecessary for $\varepsilon < 0.1$.

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia
Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

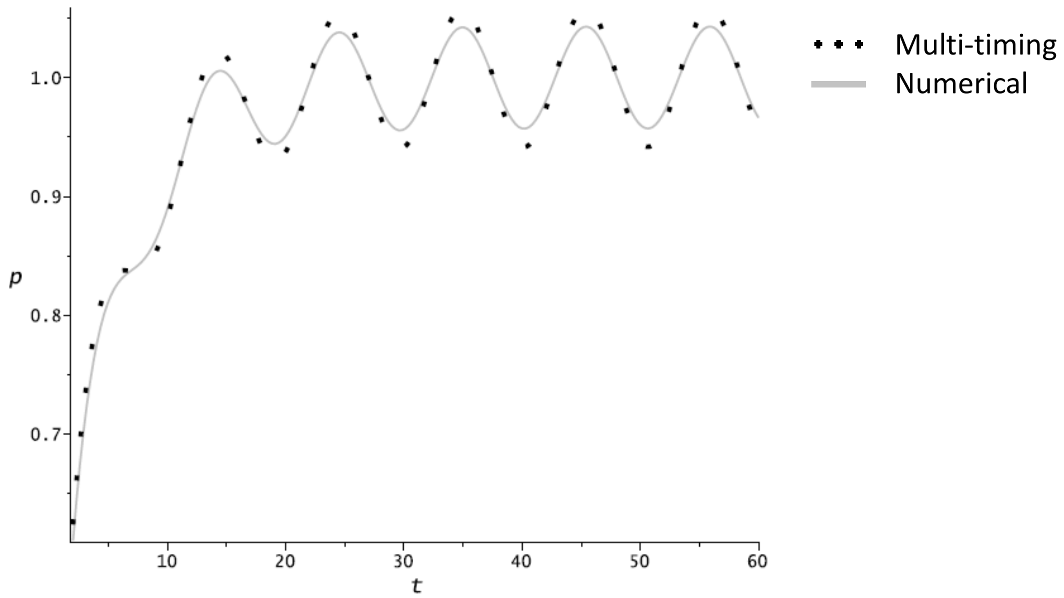

Figure 3: Plot of the multitime approximation against numerical solution for $\varepsilon = 0.05$ *varying harvesting parameter* $(e = \exp(-t_1))$ *and carrying capacity* $(k = 1 + 0.05\sin(3t_1))$

Summary

The addition of a density dependant harvesting term to the Gompertz model varies the limiting value, though no value of *E* drives the population to zero in infinite time. The model remains strictly increasing or decreasing even with a harvesting term.

The multitiming method was successful in giving an accurate approximation for the model where all parameters were varied slowly with time. This method highlights the trends of the model in terms of known parameters, unlike numerical methods. In cases where the ratio of the population time scale to the *E, R* and *K* time scales was too large we observed a significant loss of accuracy. For these cases, it would be more appropriate to extend the perturbation expansion up to higher powers of ε.

Postal Address: Building 161
c/- The University of Melbourne
Victoria 3010 Australia

Email: enquiries@amsi.org.au
Phone: +61 3 8344 1777
Fax: +61 3 8344 6324
Web: www.amsi.org.au

References

[1] Gompertz, B., 1825. On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philosophical Transactions of the Royal Society of London*, vol 115, pp. 513-583.

[2] Laird, A. K., 1964. Dynamics of Tumor Growth. *British Journal of Cancer*, 18.3, pp. 490.

[3] Grozdanovski, T., Shepherd, J. J., 2005. Slow Variation in the Gompertz Model. *ANZIAM J.*, 47, pp. C541- C554

[4] Murdock, J.A., Perturbations Theory and Methods, Society for Industrial and Applied Mathematics, USA, 1999. pp. C543