Logistic equation with a simple stochastic carrying capacity

C. Anderson[1] Z. Jovanoski[2] H. S. Sidhu[3]
I. N. Towers[4]

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Abstract

The logistic model has long been used in ecological modelling for its simplicity and effectiveness. Variations on the logistic model are prolific but, to date, there are a limited number of models that incorporate the stochastic nature of the carrying capacity. This study proposes a modification to the logistic model to incorporate a second differential equation which describes the changes in the carrying capacity, thus treating the carrying capacity as a state variable. The carrying capacity is modelled via a stochastic differential equation that accounts for stochastic ('noisy') variations in the finite resources that the population relies on. The extinction probability distribution, expected solution

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paths, variance of the solution paths, and distribution of the population are computed using the Monte Carlo method.

Contents

1 Introduction

The origins of population growth models are traced back to Malthus' influential exponential model and later to Verhulst's logistic model [1]. The logistic model acknowledges the reality of finite resources that cannot support exponential growth indefinitely. Central to this limitation is the concept of a 'saturation level' or carrying capacity—the maximum population level that an environment can support given finite resources [2]. The logistic equation is

$$\frac{dN_t}{dt} = rN_t\left(1 - \frac{N_t}{K}\right), \tag{1}$$

where N_t is the population size at time t, r is the intrinsic growth rate and K is the carrying capacity. The logistic equation has been adapted and modified for over a century. Tsoularis and Wallace [3] summarise some of these adaptations.

The carrying capacity is assumed to be constant in population growth models used for resource assessment and management [4]. However, changes to the carrying capacity do occur due to both exogenic and endogenic processes [5]. Cushing [6] and Coleman [7] recognised the need to treat the carrying capacity as a function of time to model population dynamics in an environment that undergoes change. Most populations experience fluctuations in their environment due to seasonal change [8].

The simplest approach is to specify some time dependent function for the carrying capacity that reflects the observed behaviour of the changing environment [1, 9]. However, this approach is quite limiting as it does not allow for the more realistic portrayal of the environment, and therefore its carrying capacity is not "shaped by processes and interdependent relationships between finite resources and the consumers of those resources" [10]. To mitigate this issue, Safuan et al. [11, 12, 13, 14] developed models that treat the carrying capacity as a state variable, thereby coupling the carrying capacity directly to the population.

The variations to the logistic equation mentioned thus far have their applications; however, there are many external environmental effects like fire, drought, floods and contamination of water resources, that also need to be accounted for. By adding stochasticity (noise) to the logistic equation, it is possible to account for these anomalous impacts on population dynamics that deterministic models often ignore.

How stochasticity is incorporated in population models is a modelling issue. One approach is to explicitly write the carrying capacity as consisting of a deterministic and a stochastic term [15]. More generally, environmental fluctuations are modelled by adding noise to the competition term (reciprocal of K) leading to the stochastic differential equation (SDE) [16]

$$dN_t = rN_t\left(1 - \frac{N_t}{K}\right)dt + r\sigma N_t^2\, dW_t\,, \tag{2}$$

where W_t is a standard Weiner process with mean $E[W_t] = 0$ and variance $V[W_t] = t$. The noise intensity is σ. In Section 2 we propose a different approach by treating the carrying capacity as a state variable.

2 The model

The simplest model that treats the carrying capacity as a state variable is

$$\frac{dN_t}{dt} = rN_t\left(1 - \frac{N_t}{K_t}\right), \quad N_{t=0} = N_0\,, \tag{3}$$

$$dK_t = \sigma\, dW_t\,, \quad K_{t=0} = K_0\,. \tag{4}$$

Equation (3) is just the standard logistic equation (1) describing the growth of a population as it responds to the fluctuations of K_t. Equation (4) defines the carrying capacity by a simple SDE, where σ is the intensity of the noise. Equation (4) is solved independently from (3), the solution is

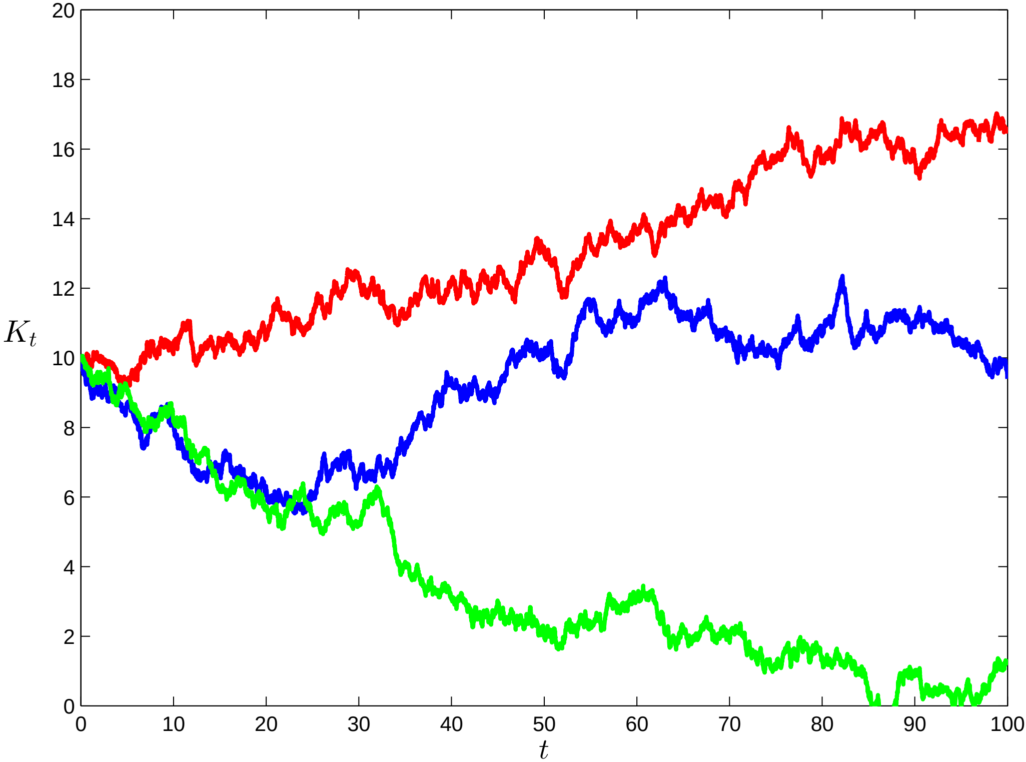
$$K_t = K_0 + \sigma W_t\,. \tag{5}$$

Substituting (5) into (3), we get

$$\frac{dN_t}{dt} = rN_t\left(1 - \frac{N_t}{K_0 + \sigma W_t}\right). \tag{6}$$

Three different realisations (simulations) of (5) are shown in Figure 1. Although this model appears simple, it may find useful applications in certain ecosystems. For example, W_t may be a proxy variable for excess rainfall over an ecosystem and then average rainfall sustains the carrying capacity at K_0.

Figure 1: Three different realisations of K_t with $K_0 = 10$ and $\sigma = 0.4$.



When $W_t > 0$, above average rainfall contributes to an increase in the carrying capacity. On the other hand, when $W_t < 0$, below average rainfall results in a decrease in the carrying capacity. Figure 1 shows a realisation (green) with a deteriorating carrying capacity that is a result of successive periods of below average rainfall: the ecosystem is experiencing a drought. If $K_t = 0$, then the environment cannot sustain a population, leading to the population's extinction. Predicting extinction times and their causes is very important for conservation [17].

3 Solution for the population size

An exact solution to (6) is currently not known. A numerical solution can be obtained once W_t is generated. Alternatively, the method used here is to numerically solve the coupled SDEs (3) and (4) using the Euler–Maruyama method. Higham [18] described this method and its strong and weak convergence in detail. Here we use graphical data analysis methods, especially quantile-quantile (qq-) plots to investigate the distributions of K_t and N_t. A step size of $\Delta t = 0.01$ was used. Smaller step sizes did not make any difference to the qq-plots. However, in generating several thousand simulations, there was a noticeable increase in computer running time when using smaller step sizes. A step size of 0.01 seemed a reasonable compromise.

3.1 Varying the intrinsic growth rate

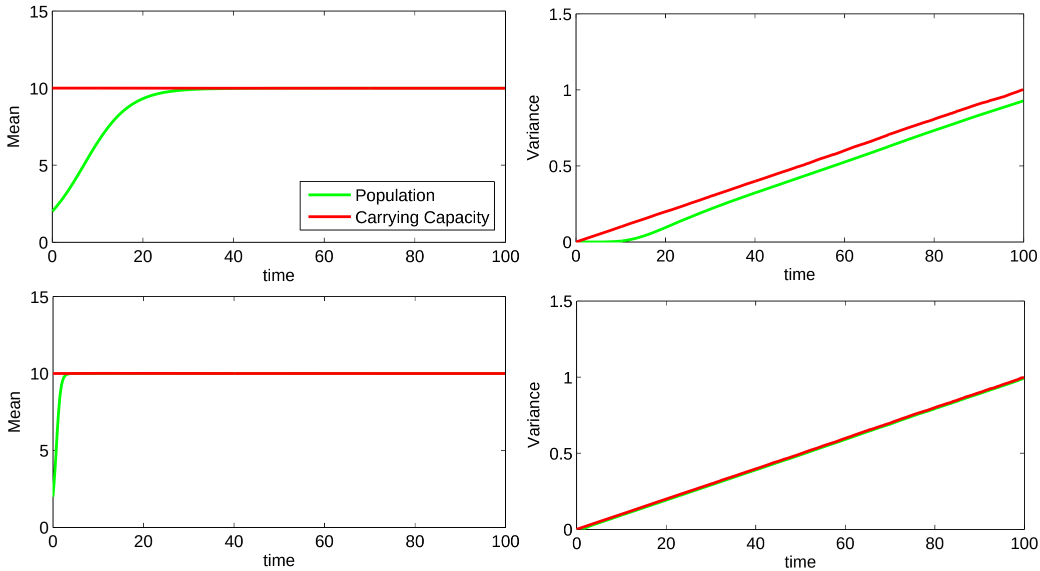
From the differential equation for N_t we have: $N_t' < 0$ if $K_t < N_t$; $N_t' = 0$ if $K_t = N_t$; and $N_t' > 0$ if $K_t > N_t$. This means that N_t will tend to follow K_t—when K_t is higher, N_t will increase towards K_t, and when K_t is lower, N_t will decrease towards K_t. In the case where the intrinsic growth rate r is large, the rate of change of N_t will be large in magnitude so it will follow K_t closely. The solution for N_t is smoother for smaller values of r—the population is less affected by rapid changes to the carrying capacity.

3.2 Expected solution path

Since $W_t \sim N(0, t)$ and as K_t is a linear transformation of W_t, $K_t \sim N\left(K_0, \sigma^2 t\right)$. From an ecological perspective, this distribution is technically not correct since $K_t > 0$. The exact (conditional) probability density function for $K_t > 0$ is

$$P_K(K, t \mid K_0) = \frac{1}{\sigma\sqrt{2\pi t}}\left[\exp\left(-\frac{(K-K_0)^2}{2\sigma^2 t}\right) - \exp\left(-\frac{(K+K_0)^2}{2\sigma^2 t}\right)\right]. \quad (7)$$

Figure 2: The effect of varying r on the mean (left) and variance (right) of the population with $K_0 = 10$, $\sigma = 0.1$ and $N_0 = 2$. In the top plots $r = 0.2$ and for the bottom plots $r = 2$.

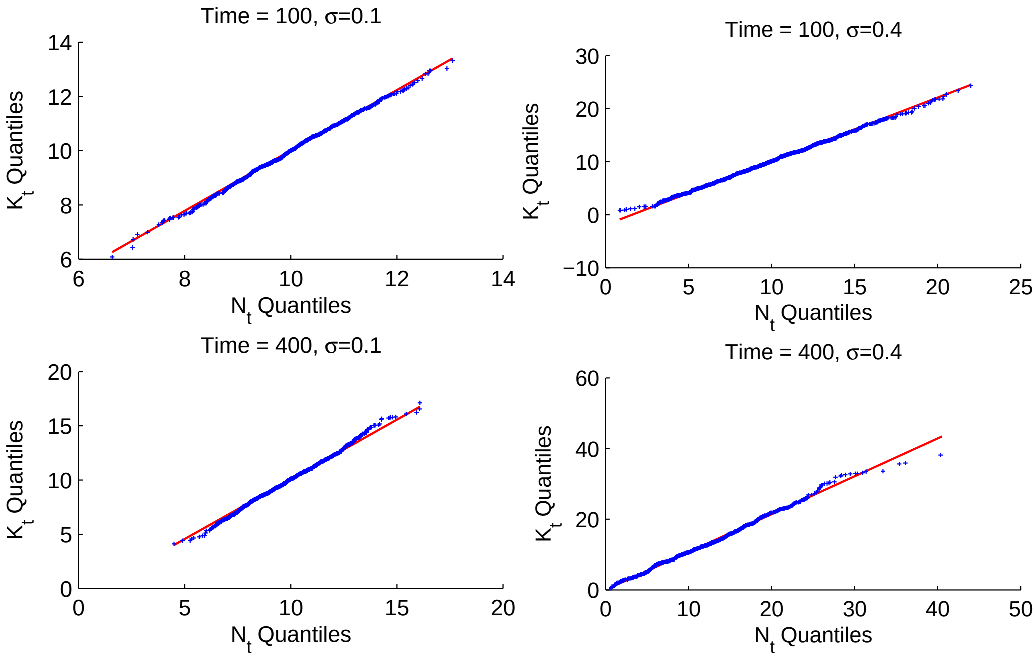


Since N_t pursues K_t, this suggests that the population has (asymptotically) a similar distribution to that of the carrying capacity: $P_N(N, t \mid N_0) \approx P_K(K, t \mid K_0)$. To investigate this we employed a Monte Carlo approach and calculated the mean and variance from 2000 simulations. Figure 2 supports the idea that the population has a mean and variance that closely match the mean and variance of the carrying capacity. A smaller value of r does not affect the mean asymptotically approaching K_0, but does slightly reduce the variance.

4 Distribution of the population size

From the numerical simulations, beyond the initial transient behaviour, N_t follows K_t closely. The expected value and variance of N_t also closely follow K_t.

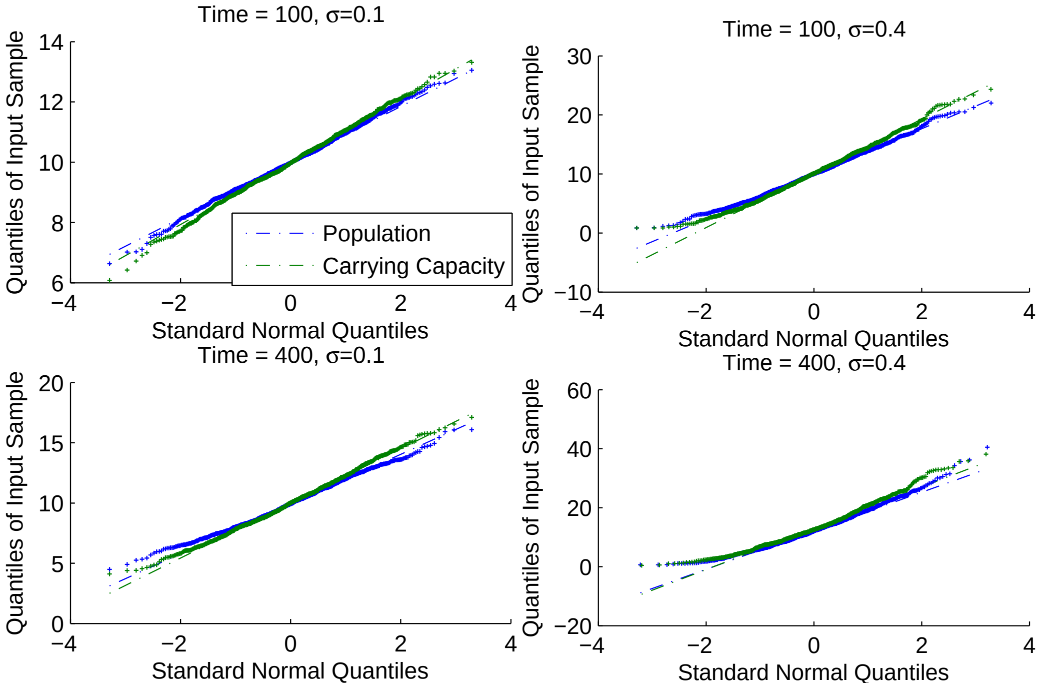
Figure 3: The qq-plots of distributions for K_t and N_t with $K_0 = 10$, $r = 0.2$ and $N_0 = 2$.



This suggests that N_t and K_t may have the same distribution. To establish if the distributions of N_t and K_t are the same, the qq-plots in Figure 3 were produced for $t = 100$ and $t = 400$ with $\sigma = 0.1$ and $\sigma = 0.4$. A qq-plot is a non-parametric method for comparing two probability distributions by plotting the quantiles against each other. The closer the quantiles on a qq-plot are to a straight line, the more likely they belong to the same distribution. For the given times and noise intensity σ, the distributions of N_t and K_t are likely to be the same.

Using qq-plots, Figure 4 compares the distributions of N_t and K_t. For times $t = 100$ and $t = 400$ with $\sigma = 0.1$ the distributions of K_t and N_t are likely to be normally distributed. The quantiles for both K_t and N_t lie on the dashed

Figure 4: The qq-plots showing if the distributions K_t and N_t are normally distributed, with $K_0 = 10$, $r = 0.2$ and $N_0 = 2$.



straight line. For small enough σ and large enough K_0 the second term in (7) is small and the assumption of normality holds true for a restricted amount of time.

When $\sigma = 0.4$ (right plots of Figure 4), as time increases, the tails of the qq-plots become noticeably less linear, especially for smaller standard normal quantiles. This indicates that the distributions for K_t and N_t are skewed. This is because, as time passes, more and more of the realisations of K_t, and subsequently N_t, are truncated at zero instead of continuing into negative values. The truncation is necessary as negative values for population and carrying capacity have no physical meaning. This is seen from (7) which gives $P_K(0, t \mid K_0) = 0$.

5 Distribution of extinction times

Recall that $K_t = K_0 + \sigma W_t$ is a scaled Wiener process with mean K_0. The first-hitting time, when the carrying capacity reaches zero, is $\tau = \inf\{t : K_t = 0\}$, and is equivalent to $\tau = \inf\{t : W_t = -K_0/\sigma\}$. For our problem, the distribution of first-hitting times is well known and is [19]

$$f_\tau(t) = \frac{K_0}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{K_0^2}{2\sigma^2 t}\right). \tag{8}$$

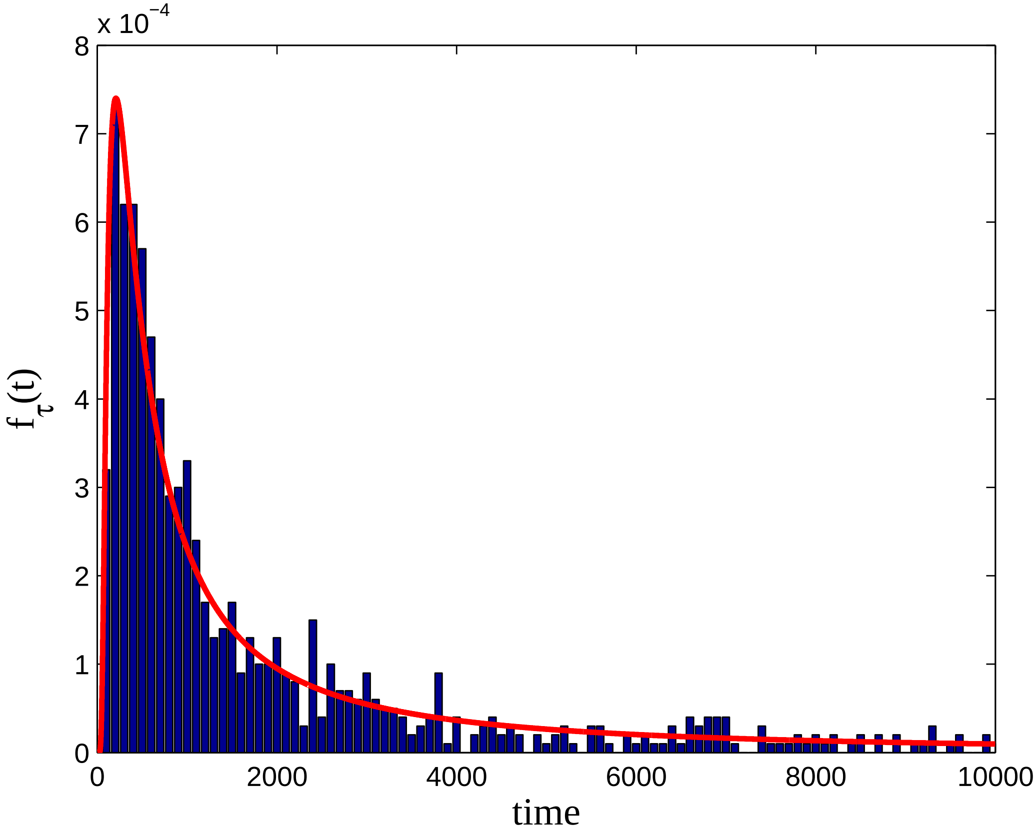
Figure 5 compares the theoretical distribution of first-hitting times with the numerically calculated equivalent. The simulations indicate that the first-hitting times for K_t satisfy (8). Furthermore, extensive numerical simulations indicated that the first-hitting times for N_t may be approximated by those for K_t.

6 Conclusion

This study investigated the implications of coupling a simple SDE describing the random variations in environmental conditions to the standard logistic equation. Through numerical simulations we showed that the population N_t defined by (3) will always pursue K_t, suggesting that the distributions are approximately the same. Beyond the transient, the means of N_t and K_t are the same and the variance of the population is slightly reduced compared to that of the carrying capacity: the reduction being larger for smaller values of r. Nevertheless, for smaller values of r the population is not strongly affected by the extremes that the carrying capacity may experience, thus the population size remains more stable compared to populations with large r.

Furthermore, in our simulations we demonstrated that for small σ and large K_0 the distribution for K_t is approximately normal. Since $K_t > 0$ the distribution is certainly not normal. Both K_t and N_t are better approximated by a skewed

Figure 5: The theoretical distribution function (curve) and the numerical probability distribution function (histograms) of the first-hitting time for K_t with $K_0 = 10$, $r = 0.2$, $N_0 = 2$ and $\sigma = 0.1$.



distribution, such as equation (7). A full analysis requires the construction and solution of the Fokker–Planck equation associated with (3) and with appropriate boundary conditions [19]. The analysis of the Fokker–Planck equation would be formidable. It may be possible to make algebraic progress in the cases where r is very large and when $0 < r \ll 1$. This is currently under investigation. Further development in this area includes models for K_t that are more realistic, such as ones that include both a deterministic and a stochastic term.

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Author addresses

1. **C. Anderson**, Applied and Industrial Mathematics Research Group in the School of Physical, Environmental and Mathematical Sciences, University of New South Wales, Canberra 2600, Australia. mailto:c.anderson@adfa.edu.au
2. **Z. Jovanoski**, Applied and Industrial Mathematics Research Group in the School of Physical, Environmental and Mathematical Sciences, University of New South Wales, Canberra 2600, Australia. mailto:z.jovanoski@adfa.edu.au
3. **H. S. Sidhu**, Applied and Industrial Mathematics Research Group in the School of Physical, Environmental and Mathematical Sciences, University of New South Wales, Canberra 2600, Australia.

mailto:h.sidhu@adfa.edu.au

4. **I. N. Towers**, Applied and Industrial Mathematics Research Group in the School of Physical, Environmental and Mathematical Sciences, University of New South Wales, Canberra 2600, Australia.
mailto:i.towers@adfa.edu.au