

Population Dynamics in a stochastic environment

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POPULATION DYNAMICS IN A STOCHASTIC ENVIRONMENT

A THESIS SUBMITTED FOR THE DEGREE OF MASTER OF PHILOSOPHY

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Abstract

When modelling population dynamics within an ecosystem, there are many factors that need to be considered, these include; birth and death rates, intra-species competition, migration, resources available, environmental conditions and predation. With so many aspects that need to be considered, many of which are constantly changing, population models quickly become very complicated. Often, in an attempt to reduce complexity, many of these factors are either ignored or overly simplified.

One of the most fundamental approaches to population modelling, based on the logistic differential equation, bundles many of these factors as demographic (the intrinsic growth rate) and environmental (through the carrying capacity). Current models treat both the demographic and environmental factors as constants. Whilst this simplifies the modelling process, it is well known that both demographic and environmental factors change with time, which in turn affects the population dynamics.

Of particular importance are environmental fluctuations. Recent attempts to model environmental fluctuations as time-dependent variables have demonstrated an increased complexity in population dynamics. However, environmental fluctuations cannot completely be characterised by time-dependent functions alone, the environment is also subjected to random and unpredictable perturbations and should be modelled accordingly.

This thesis is an investigation into population dynamics that are the result of random environmental fluctuations. Here, the carrying capacity (the maximum population an environment can sustain) is treated as a proxy for the state of the environment. The environment is allowed to vary according to a Wiener and as an Ornstein-Uhlenbeck process with an appropriate absorbing boundary condition ensuring that the carrying capacity must remain positive for the population to remain viable. For both processes, the exact probability density function for the carrying capacity is found.

The statistical properties of the carrying capacity and the population are analysed using the Monte Carlo method giving: the expected time evolution of the population and its variance, the probability distribution of the population and the mean-time to extinction.

Finally, future developments are discussed that include, among others, the effects of environmental stochasticity on the strength of the interaction between competing populations.

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Published work

The following publications correspond to work within this thesis:

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- C. Anderson, Z. Jovanoski, H. S. Sidhu and I. N. Towers, *Logistic equation with a simple stochastic carrying capacity* ANZIAM J., 56, pp. c431-c445, 2016. http://journal.austms.org.au/ojs/index.php/ANZIAMJ/article/view/9386

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CHAPTER 1

A survey of population models

The concepts of ecological modelling and carrying capacity is introduced, and some common models and recent developments are reviewed. Continuous time stochastic population models and the motivation for using them is presented.

Purpose of ecological modelling

Ecological modelling has a wide variety of applications, and it is an important tool in environmental and resource management. It may be used to assess the survival or possible extinction of a species or ecosystem by evaluating the potential impact of changes to the environment. For example, chemical exposure from the use of pesticides or fertilisers in the environment, either by direct application in an ecosystem or due to drift, run-off or spillage, has significant ramifications for an ecosystem and its biodiversity. Other possible sources of chemical exposure are industrial operations and oil spills in the ocean. Such exposure may have a negative impact on a species' habitat, possibly threatening the survival of the species.

Invasive species, of both flora and fauna, are other well-known factors that can change an environment and provide competition for resources with endemic species. A similar situation may also occur in agriculture, where native animals may be considered pests because they compete with stock for feed. The introduction of disease into an environment may also have negative impacts on the survival of a given species. A well-known example of this is the Tasmanian devil facial tumor disease, which is a transmittable cancer that has caused the species to become endangered after a significant decline in the wild population. Another source of change in the environment that impacts both the survival and distribution of species is climate change, with research on its potential impacts having increased significantly in recent years [2].

Ecological modelling has provided insight into the potential impact changes in the environment have on the survival of a given species. It aids the policy development to best manage changes as they occur, providing predictions in ecosystem dynamics and guidance in assessing the significance of changes. Plans may be developed to respond to changes and minimise their impact based on mathematical models, or steps may be taken to mitigate the likelihood of significant changes in the environment.

Models with constant carrying capacity

The concept of carrying capacity was observed by the English scholar, Malthus [3], as the "strong law of necessity acting as a check upon the greater power" of population increase. This is simply illustrated in nature, where plants and animals are driven by instinct to breed to ensure perpetuation of the species, but in which growth is kept in check by limited resources. In general, carrying capacity is considered to be the maximum population an environment can sustain. In ecology, it is regarded as a proxy for the state of the environment, often related to the availability of food, water, space or other resources, or to the impact of pollutants having a detrimental effect on the environment [4].

The Logistic model

Carrying capacity was first incorporated into a mathematical model by the Belgian mathematician, Verhulst [5], as a limit on exponential population growth. This renders the classic logistic equation [6]

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K_0}\right), \quad N(0) = N_0, \tag{1.1}$$

where $N(t) \equiv N_t$ is the population of a given species at time t, r is the intrinsic growth rate and K_0 is the constant carrying capacity. N_0 is the population at time t = 0. The exponential growth of the population, given by rN, is limited by intraspecies competition for resources described by the term $-rN^2/K_0$. The ratio r/K_0 is also referred to as the *crowding* coefficient.

Equation (1.1) is autonomous, since r and K_0 are constants, and the solution may be obtained using either separation of variables or Bernoulli's method to give

$$N_t = \frac{N_0 K_0}{N_0 (1 - e^{-rt}) + K_0 e^{-rt}}.$$
(1.2)

Figure (1.1) shows solutions of equation (1.1) for various initial conditions N_0 and growth rates r. It is clear that all solutions converge monotonically to the carrying

capacity K_0 . For very small values of N_0 , the population increases slowly at first, until it reaches a point of inflection at $N_t = K_0/2$, where the rate of increase is at its greatest. It then slows as the population asymptotically approaches the carrying capacity from below. For values of N_0 greater than $K_0/2$ but less than K_0 , the rate of increase of the population is gradual as it approaches the carrying capacity K_0 . When the initial population is greater than the carrying capacity, the population decreases rapidly at first before it gradually asymptotes to K_0 .



Figure 1.1: Plots of the logistic model, equation (1.1), for various values of r and N_0 , with $K_0 = 1$.

The logistic model was also used to estimate the population of the United States in intercensal years [7]. It also became a basis for many estimates of the maximum sustainable population of the Earth. Vandermeer [8] conducted experiments in which he expected to show ecological models need to take into account higherorder interactions to be accurate and useful. However, he found against his own prejudice that simple models such as equation (1.1) can in some circumstances be excellent predictors of population dynamics, despite failing to include higher-order interactions. However, in general, this model with its constant carrying capacity does not successfully represent reality, as physical and biological processes change the environment, in turn changing the carrying capacity for a given species.

In many applications, there is an underlying assumption that a finite level of resources implies a fixed level of resources. In particular, in resource management the carrying capacity is often assumed to be constant and unchanging [4]. Many efforts to predict the world's carrying capacity, the maximum sustainable population, are based on this assumption [9]. However, innovations and developments in technology have raised crop yields, allowing a greater population to be supported by a given land area [10]. As such, technology is changing the carrying capacity of the Earth, and that for human populations, a constant carrying capacity is not realistic [11]. Similarly in nature, the inherent variability of natural systems means that an unchanging carrying capacity fails to adequately represent the environment [12].

The general assumption of a constant carrying capacity was challenged by del Monte-Luna et al. [4] through an analysis of the different ways it is applied to populations, communities, ecosystems and the biosphere, and proposed the following definition for carrying capacity:

"the limit of growth or development of each and all hierarchical levels of biological interaction, beginning with the population, and shaped by processes and interdependent relationships between finite resources and the consumers of these resources".

This definition highlights the importance of defining the carrying capacity in a mathematical model so that it may vary with time. Such a treatment of the concept allows a more realistic portrayal of the way in which various processes and relationships, both biotic and abiotic, influence the environment.

Models with a time-dependent carrying capacity

In this Section we relax the requirement that the carrying capacity be a fixed quantity. There are many situations involving the evolution of a population in which the carrying capacity changes with time. The starting point is a brief description of the well known Jillson experiment.

Experimental example of environmental periodicity

Periodic fluctuations in the environment have been observed to influence populations, both detrimentally and advantageously. A specific example of this was demonstrated by Jillson [1], in which the responses of populations of the red flour beetle, *Tribolium castaneum*, were examined under the influence of a periodic environment. A culture medium providing food for the beetles of 95% unbleached wheat flour and 5% brewers yeast (by weight) was provided for thirty separate populations of 30 adults (with a 1:1 sex ratio) and 75 unsexed small larvae. For the first eighteen weeks of the experiment, each population was subject to a constant environment with 20 g of medium. At week eighteen, five different experimental regimes were commenced, with six populations undergoing each regime. The first was a control, with the medium kept at a constant 20 g for the duration of the experiment. The remaining populations were subject to periodic fluctuations in the amount of medium, either 32 g or 8 g. The period for each regime was 4 weeks, 8 weeks, 12 weeks or 16 weeks. A census was taken of the total number of animals (including adults, pupae and larvae) every two weeks, and the experiment concluded after a total of 64 weeks.

Figure (1.2) shows the results of the experiment. The control populations experienced small fluctuations, which Jillson attributed in part to cannibalistic interactions (adults and larvae will eat the eggs and pupae of their own species [13]). The population increased by an average of four animals per week. Under the four-week regime, the beetles responded much better, showing an increase of 21 animals per week up until week 54, when a decline was observed before the population began to grow again. In the 8, 12 and 16-week regimes, the populations grew during the periods of 32 g of medium, and declined in the periods of 8 g of medium.

This experiment is a clear demonstration that periodically changing the carrying capacity impacts the dynamics of the resident population. In the case of the red flour beetles, a period of four weeks proved more beneficial to the population than either a constant environment or fluctuations of longer period. Jillson suggested that that four-week oscillation in the environment was so advantageous because it suited the beetle, with high levels of recruitment during times of abundant medium, and minimising cannibalism in the leaner times with only 8 g of medium.

The dynamics observed were successfully modelled using a *discrete-time* 'LPA' model (accounting for larvae, pupae and adults, governed by separate equations) which included the volume of culture (food) available to the beetles [14]. In this manner, the changing carrying capacity was successfully modelled in a non-linear system. However, its application is limited to this specific situation. This is just one example of a population responding to a periodic environment.



Figure 1.2: Graphs from Jillson [1] showing the mean number of animals in constant and fluctuating environments. Shaded bars represent periods of 32 g of medium; intervening periods had 8 g of medium.

A Logistic model with time-dependent carrying capacity

Time-dependent carrying capacities have been successfully used in many models. In these cases, the carrying capacity is defined explicitly as a function of time, $K(t) \equiv K_t$. A periodic form of the carrying capacity, for example

$$K_t = K_0 + \epsilon \sin(\omega t), \tag{1.3}$$

might be used to represent seasonal variations in the environment, possibly influencing the amount of vegetation available for food. Models of a similar form have been used to represent population growth in a periodic environment [15, 16, 17]. Populations are known to change as a result of periodic changes in their carrying capacity. For example, in a long-term study of five commercial orchards, Aluja et al. [18] observed marked seasonal fluctuations in the populations of *Anastrepha* fruit fly species. In laboratory conditions, Jillson [1] found that populations of the red flour beetle *Tribolium castaneum* thrived far better in a periodically fluctuating environment than in a controlled environment with constant carrying capacity. Turchin and Ellner [19] found vole populations in southern Fennoscandia followed dynamics described by a model using seasonal carrying capacity with large oscillations. Multiple time scales have also been used, representing environmental fluctuations on a longer time scale than that of the population [20, 21]. Using equation (1.3) in conjunction with equation (1.1) produces the system

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

$$K_t = K_0 + \epsilon \sin(\omega t).$$
(1.4)

It is important to note that the carrying capacity is completely independent of the population, meaning that the population does not have any impact on the environment. Figure (1.3) plots two solutions to system defined by equation (1.4), with r = 1.2 and r = 5. It can be seen that both solutions tend to follow the carrying capacity curve, and while a larger growth rate r causes the population to always be much closer to the carrying capacity K_t , the solutions have the same period. As opposed to the monotonic convergence when the carrying capacity is constant, a periodic carrying capacity forces periodicity into the model for the population.



Figure 1.3: Plot of N_t against t for system equation (1.4) with $K_0 = 1$, $N_0 = 0.5$, $\omega = 1$ and $\epsilon = 0.1$.

The carrying capacity has also been represented by a saturation function, for example

$$K_t = a + b \left(1 - e^{-\alpha t} \right), \tag{1.5}$$

for which the carrying capacity monotonically increase for some lower value a to a higher value a + b. This model was used to describe the carrying capacity to model the dynamics of a fish population in a eutrophicated inland sea [22], and also used to model the total microbial biomass under an occlusion on human skin [23].

Another possibility is to represent the carrying capacity using a logistic function

$$K_t = a + \frac{b}{1 + ce^{-dt}}.$$
 (1.6)

This type of functional form for the carrying capacity was applied to model the cumulative number of nuclear tests by the US, the installed electric generating capacity of the US, and the cumulative number of publications written or edited by a colleague [24].

Defining carrying capacity explicitly as a function of time allows better modelling of changes in the environment. However, these models do not allow for a population to have an impact on its own environment. One way to overcome this is to couple the carrying capacity as a variable in a system of ordinary differential equations.

Carrying capacity as a state-variable

Even though proposing a specific functional form for the carrying capacity has proved useful, as indicted by the above examples, the main criticism is that the functional form needs to be prescribed from the outset. In a series of papers, Safuan and co-workers have argued that a better approach is to model the carrying capacity as a state-variable [23, 25, 26, 27, 28]. This approach requires that the rate of change of the carrying capacity, K_t , be expressed through a differential equation. Then the above illustrative examples of a time-dependent carrying capacities can be written as differential equations, but more importantly, it provides the flexibly to model population-environment interactions directly.

Illustrative examples

A possibility for describing carrying capacity is to define it as a state-variable, represented by an ordinary differential equation. In this case a system of equations is used, one equation for the rate of change of the population N'_t , defined by equation (1.1), and one for the rate of change of the environment's carrying capacity, K'_t . Models of this form have been successfully used in some applications. Huzimura and Matsuyama [29] used a decay model for the carrying capacity, given by

$$\frac{dK_t}{dt} = -bN_t,\tag{1.7}$$

where the rate of decay is proportional to the population. They applied it to isolated deer populations, where the carrying capacity was determined by the amount of lichen available, the main food source for the deer. With only small hunting pressure and no predation of the deer due to isolation on an island, this model was found to produce estimates accurate to within 10% of the actual deer population.

A bilogistic model, expressing the carrying capacity with a logistic differential equation

$$\frac{dK_t}{dt} = bK_t \left(1 - \frac{K_t}{K_0}\right) \tag{1.8}$$

was applied to the human populations of Japan and England, as affected by the increase in carrying capacity that resulted from the industrial revolution [11].

An interaction model of the form

$$\frac{dK_t}{dt} = bK_t - cK_t N_t \tag{1.9}$$

was more recently developed to allow for the interaction between the population and its environment through the carrying capacity [25]. This model was shown to have the potential to be applied in biology and ecology, as an improvement on previous modified logistic models.

What's next?

This Chapter was concerned with continuous time processes modelled as a system of ordinary (nonlinear) differential equations. These models assume that the observed dynamics are driven exclusively by deterministic processes. However, real ecological systems are always exposed to influences that are also random. Therefore there is an increasing requirement to extend deterministic models to include stochastic (random) influences or noise. A natural extension of a deterministic differential equation is a stochastic differential equation (SDE), where relevant parameters are modelled as suitable stochastic processes, or more importantly, stochastic processes are added as driving forces. These forces may be internal to the ecological system or external to the system, or both.

All ecological systems evolve under stochastic forces. To be realistic, ecological models need to include these random influences. The justification to include random processes can be found in many ecological circumstances: variability in rainfall over a region, the intermittent release of toxins in waterways, and the occasional coral bleaching due to climate change.

It is therefore essential to investigate and understand the influence of noise on the dynamics of a population that is affected by stochastic *environmental* processes. In some cases the noise simply blurs the underlying dynamics without qualitatively affecting it. However, in many nonlinear models, the noise can dramatically change the corresponding deterministic dynamics. Stochastic effects may influence population dynamics in new and surprising ways – may enhance, diminish or even completely change the dynamical behaviour of the population.

The next Chapter provides a brief introduction to stochastic processes and to SDE.

CHAPTER 2

Stochastic Processes: Basic ideas

There exist a number of excellent textbooks that cover stochastic processes and stochastic differential equations [30, 31, 32]. This Chapter brings together the main concepts relevant to this thesis.

A random walk

A common way to introduce stochastic based modelling is to approach it from the perspective of a random walk. A (symmetric) random walk can be thought of as the path travelled when: standing at an initial starting point, a (fair) coin is tossed, should the result be heads, one step is taken to the left, conversely, should the result be tails, one step is taken to the right. Let X_t represent the location of the walker after t steps. If the initial starting point is $X_0 = 0$ and taking a step to the right is the equivalent of decreasing X_t by one and taking a step to the left is the equivalent of increasing X_t by one, then by repeatedly tossing a coin and executing the corresponding steps a random walk is generated. Figure (2.1) is a graphical representation of several realisations of a random walk. Obviously, each time the experiment is run, over a long enough time period, it will result in different realisations, this is illustrated with the different coloured paths.

To describe this mathematically, we first define the probability mass function (PMF) for the discrete random variable which describes the event of an individual coin toss. Since the result of each coin toss does not effect the result of any other coin toss, the events are considered to be independent. Thus, the random variable Y_i describing the *movement* based on the outcome of the *i*-th coin toss has PMF: $\mathbb{P}(Y_i = 1) = \mathbb{P}(Y_i = -1) = \frac{1}{2}$. This is a transformed Bernoulli distribution, $Y_i \sim 2 \cdot \text{Bern}(\frac{1}{2}) - 1$. From here, it is a straight forward to calculate the expected value $\mathbb{E}[Y_i] = 0$ and variance $\mathbb{V}[Y_i] = 1$.

The random walk is then defined as the sum of discrete steps of size *one* unit starting at the position $X_0 = 0$,

$$X_n = \sum_{i=1}^n Y_i.$$
 (2.1)

As Y_i is a transformed Bernoulli distribution, the PMF of equation (2.1) can be written as a transformed Binomial distribution

$$X_n \sim \sum_{i=1}^n \left[2 \cdot \operatorname{Bern}\left(\frac{1}{2}\right) - 1 \right] = 2 \cdot \operatorname{Bin}\left(n, \frac{1}{2}\right) - n.$$
 (2.2)

The expectation and variance of the random walk can be found from (2.1), with the expected value

$$\mathbb{E}[X_n] = \mathbb{E}\left[2 \cdot \operatorname{Bin}\left(n, \frac{1}{2}\right) - n\right] = 2 \cdot \mathbb{E}\left[\operatorname{Bin}\left(n, \frac{1}{2}\right)\right] - \mathbb{E}[n] = 2 \cdot \frac{n}{2} - n = 0 \quad (2.3)$$

and variance

$$\mathbf{\mathbb{V}}[X_n] = \mathbf{\mathbb{V}}\left[2 \cdot \operatorname{Bin}\left(n, \frac{1}{2}\right) - n\right] = 2^2 \cdot \mathbf{\mathbb{V}}\left[\operatorname{Bin}\left(n, \frac{1}{2}\right)\right] - \mathbf{\mathbb{V}}[n] = 4 \cdot \frac{n}{4} - 0 = n. \quad (2.4)$$

The expected value of a random walk can be numerically calculated by determining the mean, at every discrete time step, of many realisations. Figure (2.2) illustrates



Figure 2.1: Multiple realisations of a random walk

the convergence to the mean where an increasing number of realisations is averaged at each discrete time step and plotted on the same graph. It is clear that as the number of realisations increases, the resultant average gets closer to $\mathbb{E}[X_n] = 0$.



Figure 2.2: The expectation of an increasing number of realisations of a random walk.

The variance of many realisations of a random walk can similarly be calculated by finding the variance at every discrete time step. Figure (2.3) illustrates the convergence of the variance with an increasing number of realisations. It is clear that as the number of realisations increases, the resultant variance gets closer to $\mathbf{V}[X_n] = n$.



Figure 2.3: The variance of an increasing number of realisations of a random walk.

Wiener process

The most important stochastic process in continuous time is the Wiener process. It is used as a building block in more elaborate models. In 1828 the Scottish botanist Robert Brown observed that pollen grains suspended in water moved in an apparently random way, changing direction continuously. This was later explained by the pollen grains being bombarded by water molecules. The precise mathematical formulation to explain this phenomenon was given by Wiener in 1923.

The Wiener process can be seen as the limit of a (symmetric) random walk when the time steps and the jump sizes both approach 0. To construct a Wiener process from a random walk two small adjustments need to be made. Instead of of X_t moving up or down by one unit, it now moves a small amount Δx , and instead of making that movement every unit of time it moves every Δt units of time. This results in the probability mass function of the random variable Y_i becoming $\mathbb{P}(Y_i = \Delta x) = \mathbb{P}(Y_i = -\Delta x) = \frac{1}{2}$. Again, the expected value and variance can be calculated simply as $\mathbb{E}[Y_i] = 0$ and $\mathbb{V}(Y_i) = (\Delta x)^2$. The continuous random walk is then defined as the sum of steps of size Δt starting at the position $X_0 = 0$,

$$X_t = \sum_{i=1}^{\frac{t}{\Delta t}} Y_i. \tag{2.5}$$

As seen previously with the random walk, Y_i can be interpreted as a transformed Bernoulli distribution, the PMF of equation (2.1) can be written as a transformed Binomial distribution

$$X_t \sim \sum_{i=1}^{\frac{t}{\Delta t}} \left[2\Delta x \cdot \operatorname{Bern}\left(\frac{1}{2}\right) - \Delta x \right] = 2\Delta x \cdot \operatorname{Bin}\left(\frac{t}{\Delta t}, \frac{1}{2}\right) - \frac{t \cdot \Delta x}{\Delta t}.$$
 (2.6)

The expected value and variance of the continuous random walk with $X_0 = 0$ can be calculated as

$$\mathbb{E}[X_t] = \mathbb{E}\left[2\Delta x \cdot \operatorname{Bin}\left(\frac{t}{\Delta t}, \frac{1}{2}\right) - \frac{t \cdot \Delta x}{\Delta t}\right] = \frac{2t \cdot \Delta x}{2\Delta t} - \frac{t \cdot \Delta x}{\Delta t} = 0, \quad (2.7)$$

and

$$\Psi[X_t] = \Psi\left[2\Delta x \cdot \operatorname{Bin}\left(\frac{t}{\Delta t}, \frac{1}{2}\right) - \frac{t \cdot \Delta x}{\Delta t}\right] = \frac{4t \cdot (\Delta x)^2}{4\Delta t} - 0 = \frac{t \cdot (\Delta x)^2}{\Delta t}.$$
 (2.8)

By allowing Δx and Δt approach zero simultaneously, the continuous random walk becomes a continuous stochastic process, the Wiener process. To ensure that the variance is not zero or infinite, it is necessary for $\Delta x = \sigma \sqrt{\Delta t}$, substituting into equation (2.8), the variance becomes, $\mathbf{V}[X_t] = \sigma^2 t$, and the expected value, from equation (2.7), is $\mathbb{E}[X_t] = 0$. Here σ is a constant that describes the size of the noise. The distribution of X_t can be found by substituting $\Delta x = \sigma \sqrt{\Delta t}$ into equation (2.6) and approximating the Binomial distribution with a Normal distribution.

$$X_t \sim 2\sigma\sqrt{\Delta t} \cdot \operatorname{Bin}\left(\frac{t}{\Delta t}, \frac{1}{2}\right) - \frac{t \cdot \sigma\sqrt{\Delta t}}{\Delta t}$$
$$= 2\sigma\sqrt{\Delta t} \cdot N\left(\frac{t}{2\Delta t}, \frac{t}{4\Delta t}\right) - \frac{t \cdot \sigma\sqrt{\Delta t}}{\Delta t}$$
$$= N\left(\frac{2t \cdot \sigma\sqrt{\Delta t}}{2\Delta t} - \frac{t \cdot \sigma\sqrt{\Delta t}}{\Delta t}, \frac{4t \cdot \sigma^2 \cdot \Delta t}{4\Delta t}\right)$$
$$X_t \sim N\left(0, \sigma^2 t\right)$$

A stochastic process W_t , defined for $t \ge 0$, is called a Wiener process (or sometimes as Brownian motion) if the following conditions are satisfied:

- (a) $W_{t=0} = 0$, with probability 1,
- (b) W_t , for $t \ge 0$, has independent increments

$$W_{t_1}, W_{t_2} - W_{t_1}, \cdots, W_{t_k} - W_{t_{k-1}}$$

which are independent and identically distributed random variables for all $0 < t_1 < t_2 < \cdots < t_k$.

(c) $W_{t+s} - W_s \sim N(0, t)$ for all t > 0.

Here, $N(\mu, \sigma^2)$ denotes the normal distribution with mean μ and variance σ^2 . Thus, the Wiener process is a Gaussian process: a stochastic process X_t is called a *Gaussian process* if for any finite set of indices t_1, \ldots, t_k the vector of random variables $(X_{t_1}, \ldots, X_{t_k})$ is a k-dimensional normal distribution.

The Wiener process is continuous with mean zero and variance proportional to the elapsed time: $\mathbb{E}[W_t] = 0$ and $\mathbb{V}[W_t] = t$. If X_t is a stationary stochastic process, then X_t has the same distribution as X_{t+h} for all h > 0. Thus, the Wiener process cannot be stationary since the variance increases with t. The auto-covariance function is given by $\mathbb{C}[W_t, W_s] = \min(s, t)$. An important observation is that the sample paths of a Wiener process are continuous but are nowhere differentiable. For a technical discussion see Hanson [33].

Stochastic differential equations

Assume the ordinary differential equation

$$\frac{dx}{dt} = g(x,t) \tag{2.9}$$

describes a one-dimensional ODE. Assume that g(x,t) fulfills conditions such that a unique solution exists, thus $x(t) = x(t; x_0, t_0)$ is a solution satisfying the initial condition $x(t_0) = x_0$ [34]. Given the initial condition, we know how the ODE behaves at all subsequent times t, even when an analytic solution is not possible. Of course the ODE can be solved numerically to any desired accuracy. In many ecological applications deterministic models are not realistic, and a more realistic model allows for the inclusion of random effects.

A natural extension of a deterministic ODE model is to employ a SDE model. In this thesis random effects are introduced exclusively via the Wiener process. It leads to a differential equation with both a deterministic and a stochastic contribution,

$$dX_t = \mu(X_t, t)dt + \sigma(X_t, t)dW_t, \qquad (2.10)$$

where X_t is a stochastic process. Here W_t is a Wiener process and since it is nowhere differentiable, care is needed to define what the differential means. It turns out that it is very useful to write $dW_t = \xi_t dt$, where ξ_t is a white noise process, defined as being normally distributed for any fixed t and uncorrelated, $\mathbb{E}[\xi_t \xi_s] = 0$ if $s \neq t$. Strictly speaking, the white noise process ξ_t does not exist as a conventional function of t, but should be interpreted as the generalised derivative of a Wiener process.

A SDE in the form of equation (2.10) is said to be written in the Itô form. The functions $\mu(X_t, t)$ and $\sigma(X_t, t)$ can be nonlinear, where $\mu(X_t, t)$ is called the drift or the deterministic component (even though it may be a function of a random variable (X_t) , and $\sigma(X_t, t)$ is the diffusion part or the stochastic component. Equation (2.10) should be interpreted in the following way,

$$X_t = X_{t_0} + \int_{t_0}^t \mu(X_s, s) ds + \int_{t_0}^t \sigma(X_s, s) dW_s,$$
(2.11)

where X_{t_0} is a random variable independent of the Wiener process. It could simply be a constant. The first integral on the right hand side can be interpreted as an ordinary integral, however, the second integral is a little more problematic as the Wiener process is nowhere differentiable.

In an attempt to subscribe meaning to the definite integral

$$\int_{t_0}^t f(s)dW_s.$$
(2.12)

it is instructive to look to ordinary calculus for clues. If $f(t) \equiv \sigma$ is constant then it is reasonable to expect the integral in equation (2.12) to equal $\sigma(W_t - W_{t_0})$. Since the increments of a Wiener process has expectation 0, the above integral also has expectation equal to 0.

Now assume that f(t) is a non-random step function of the form $f(s) = \sigma_j$ on $t_j < s < t_{j+1}$ for $j = 1, 2, \dots, n$ where $t_0 = t_1 < t_2 < \dots < t_{n+1} = t$. Following on from above

$$\int_{t_0}^t f(s)dW_s \approx \sum_{j=1}^n \sigma_j (W_{t_{j+1}} - W_{t_j}).$$

It is logical to approximate a well-behaved function f(t) by a series of step functions for sufficiently small increments of t. Define a partition P_n of the interval $[t_0, t]$ by $t_0 = t_1 < t_2 < \cdots < t_{n+1} = t$ where $|P_n| = \max \{|t_{j+1} - t_j| : j = 1, \ldots, n\}$ is the norm of the partition, and approximate

$$f(t) \approx f(t_j^*)$$
 for $t_j \leq t < t_{j+1}$

where the point $t_j^* \in [t_j, t_{j+1}]$. Then define

$$\int_{t_0}^t f(s) dW_s = \lim_{|P_n| \to 0} \sum_{j=1}^n f(t_j^*) (W_{t_{j+1}} - W_{t_j}).$$
(2.13)

When f(t) is stochastic it turns out that – unlike ordinary integrals – it makes a difference how t_j^* is chosen! To see this consider the special case $f(t) = W_t$ and define two approximations: $t_j^* = t_j$, the left-end point, and $t_j^* = t_{j+1}$, the right-end point. Taking expectations of the two choices yield different results:

$$\mathbb{E}\left[\sum_{j=1}^{n} W_{t_j}(W_{t_{j+1}} - W_{t_j})\right] = \sum_{j=1}^{n} \mathbb{E}\left[W(t_j)(W_{t_{j+1}} - W_{t_j})\right]$$
$$= \sum_{j=1}^{n} \mathbb{E}\left[W_{t_j}\right] \mathbb{E}\left[(W_{t_{j+1}} - W_{t_j})\right] = 0$$

using condition (c). On the other hand,

$$\mathbb{E}\left[\sum_{j=1}^{n} W_{t_{j+1}}(W_{t_{j+1}} - W_{t_{j}})\right] = \mathbb{E}\sum_{j=1}^{n} \left[(W_{t_{j+1}} - W_{t_{j}})^{2}\right] \\ + \mathbb{E}\sum_{j=1}^{n} \left[W_{t_{j}}(W_{t_{j+1}} - W_{t_{j}})\right] \\ = \sum_{j=1}^{n} \mathbb{E}\left[(W_{t_{j+1}} - W_{t_{j}})^{2}\right] + 0 \\ = \sum_{j=1}^{n} (t_{j+1} - t_{j}) = t - t_{0}.$$

Two useful and common choices are the following,

- (a) The Ito integral: $t_j^* = t_j$, the left-end point.
- (b) The Stratonovich integral: $t_j^* = (t_j + t_{j+1})/2$, the mid-point.

There are arguments for using either one or the other, most of them rather technical [30]. In this thesis only the Ito interpretation of the stochastic integral is used.

Some important examples

Three important stochastic processes are considered, all expressed in the Ito form.

Example 1 – Wiener process with drift

Imagine the pollen grain, mentioned earlier, suspended in water which is subject to the constant bombardment of water molecules. The temperature of the water influences the momentum of the water molecules which in turn determines the force of the bombardment. A parameter, say σ is needed to characterise the strength of this force. Assume there exists a water current which drives the pollen grain in a certain direction, and assume the parameter μ characterises the drift. The SDE that describe this stochastic process is

$$dX_t = \mu dt + \sigma dW_t, \tag{2.14}$$

which has the solution

$$X_t = \mu t + \sigma W_t. \tag{2.15}$$

Then X_t is normally distributed with mean, $\mathbb{E}[X_t] = \mu t + \sigma \mathbb{E}[W_t] = \mu t$, and variance, $\mathbb{V}[X_t] = \sigma^2 \mathbb{V}[W_t] = \sigma^2 t$.

Example 2 – Geometric Brownian motion

Suppose a drug is injected into the blood stream and that the *average* metabolic process of the drug is modelled as exponential decay through the deterministic equation x' = -kx, where x is the concentration of the drug and k is the decay rate. Suppose now that the decay rate fluctuates randomly due the enzymatic action involved in the breakdown of the drug. Such a scenario could be modelled by allowing k to vary randomly, $k = \mu + \sigma \xi_t$, where ξ_t is a Gaussian white noise process.

Then $\xi_t dt$ can be written as the differential of a Wiener process, dW_t . This leads to the model

$$dX_t = -\mu X_t dt + \sigma X_t dW_t. \tag{2.16}$$

Later, it is shown that the explicit solution is

$$X_t = X_0 \exp\left(-\left(\mu + \frac{1}{2}\sigma^2\right)t + \sigma W_t\right).$$
(2.17)

The process only takes positive values and X_t follows a log-normal distribution with parameters $-(\mu + \sigma^2/2)t$ and $\sigma^2 t$.

Example 3 – Ornstein-Uhlenbeck process

Imagine a process subject to a restoring force, that is, the process is attracted to some constant level but is continuously perturbed by noise. An example is given by the membrane potential of a neuron that is constantly being perturbed by electrical impulses from the surrounding network, and at the same time is attracted to an equilibrium value depending on the resting potentials for different ions present at different concentrations inside the cell and in the interstitium. This leads to the model

$$dX_t = -\gamma (X_t - \alpha)dt + \sigma dW_t.$$
(2.18)

Here $1/\gamma$ has units of time, and is the typical time constant of the process. The autocorrelation is given by $\mathbb{E}[X_t X_{t+s}] = e^{-\gamma s}$, and thus the autocorrelation has decreased with a factor of e^{-1} after $1/\gamma$ units of time. It has the explicit solution

$$X_t = X_0 e^{-\gamma t} + \alpha (1 - e^{-\gamma t}) + \int_0^t \sigma e^{-\gamma (t-s)} dW_s.$$
 (2.19)

The stochastic process X_t (given X_0) is normally distributed with mean $\mathbb{E}[X_t|X_0] = X_0 e^{-\gamma t} + \alpha (1 - e^{-\gamma t})$ and variance $\mathbb{V}[X_t|X_0] = \sigma^2 (1 - e^{-2\gamma t})/(2\gamma)$.

When the diffusion term does not depend on the state-variable X_t , such as in the Wiener process with drift and the Ornstein-Uhlenbeck process, the noise is said to be *additive*. In the case of Geometric Brownian motion the noise is said to *multiplicative*.

Stochastic chain rule (Itô's formula)

Stochastic differentials do not obey the ordinary chain rule as we know it from classical calculus. To see this let X_t be a stochastic process given by

$$dX_t = \mu(t, X_t)dt + \sigma(t, X_t)dW_t,$$

and let f(t, x) be a sufficiently smooth and differential function in x and t. Then

$$Y_t = f(t, X_t)$$

is also a stochastic process that satisfies

$$dY_t = \frac{\partial f}{\partial t}(t, X_t)dt + \frac{\partial f}{\partial X_t}(t, X_t)dX_t + \frac{1}{2}\sigma^2(t, X_t)\frac{\partial^2 f}{\partial X_t^2}(t, X_t)dt.$$
 (2.20)

Note that the first two terms on the right hand side correspond to the chain rule we know from classical calculus, but an extra term appears in stochastic calculus because the Wiener process $(dW_t)^2$ behaves like dt.

As an illustrative example, consider the SDE of the Geometric Brownian motion given by equation (2.16). Rewrite the equation as

$$\frac{dX_t}{X_t} = -\mu dt + \sigma dW_t. \tag{2.21}$$

Thus, integrating

$$\int_0^t \frac{dX_s}{X_s} = -\mu t + \sigma W_t, \qquad (2.22)$$

which suggests the transformation $Y_t = \ln(X_t)$ with $Y_0 = \ln(X_0)$. Applying the Ito formula leads to

$$dY_t = d(\ln X_t) = 0 + \frac{dX_t}{X_t} + \frac{1}{2}\sigma^2 X_t^2 \left(-\frac{1}{X_t^2}\right) dt = \frac{dX_t}{X_t} - \frac{1}{2}\sigma^2 dt.$$

Substituting equation (2.16) into the above equation

$$dY_t = -\left(\mu + \frac{\sigma^2}{2}\right)dt + \sigma dW_t,$$

whose solution is

$$Y_t = Y_0 - \left(\mu + \frac{\sigma^2}{2}\right)t + \sigma W_t.$$

Transforming back to the original process X_t ,

$$X_t = X_0 \exp\left(-\left(\mu + \frac{1}{2}\sigma^2\right)t + \sigma W_t\right).$$
(2.23)

Numerical solution: The Euler-Maruyama scheme

When no explicit solution is available it is possible to approximate different characteristics of the process by simulation, such as sample paths, moments, qualitative behavior etc. Usually such simulation are based on discrete approximations of the continuous solution to the governing SDE. Different schemes are available depending on how good the approximation is required to be, which comes at a price of computer time.

Suppose an approximate solution to equation (2.10) is sought over the time interval [0, T]. Consider the time discretisation

$$0 = t_0 < t_1 < \dots < t_j < \dots < t_n = T$$

and denote the time steps by $\Delta t_j = t_{j+1} - t_j$ and the increments of the Wiener process by $\Delta W_j = W_{t_{j+1}} - W_{t_j}$. Then $\Delta W_j \sim N(0, \Delta t_j)$, which can be used to construct approximations by generating normally distributed numbers, a trivial task for modern software packages such as MATLAB.

For simplicity consider a time-homogenous process, one for which t does not explicitly appear in the SDE. The simplest scheme is the stochastic analogue of the deterministic Euler scheme. Approximate the process X_t at the discrete time-points t_j , $1 \le j < n$ by the recursion

$$\hat{X}_{t_{j+1}} = \hat{X}_{t_j} + \mu(\hat{X}_{t_j})\Delta t_j + \sigma(\hat{X}_{t_j})\Delta W_j$$
, with $\hat{X}_{t_0} = x_0$

where $\Delta W_j = \sqrt{\Delta t_j} Z_j$, with Z_j being a *standard* normal variable with mean 0 and variance 1 for all j. The scheme can be easily implemented in MATLAB. The code for simulating a trajectory of a Geometric Brownian motion over the time interval

[0, T] is given below [35]. This code, and its adaptation to other applications, is used extensively throughout this thesis.

```
clear all;
x0 = 1; \% initial condition
beta = -0.5; sigma = 0.5; % parameter values
n = 1000; % number of discretization points
T = 1; % length of simulation interval
dt = T/n; % size of time step
randn('state',0); % sets the seed of the random number generator
% simulate a trajectory
x_euler = zeros(n+1,1); % initialization of the trajectory
x_{euler}(1) = x0; % the initial condition
for j=2:n+1 % the Euler-Maruyama scheme
dW = sqrt(dt)*randn; % the Wiener increment
x = x_{euler(j-1)};
x_euler(j) = x + beta*x*dt + sigma*x*dW;
end
% plot the approximation
figure
plot([0:dt:1],x_euler,'k-')
xlabel('t')
title('Euler-Mayurama approximation of GBM')
```

This approximating procedure assumes that the drift and diffusion functions are constant between time steps, so obviously the approximation improves for smaller time steps. To evaluate the convergence things are more complicated for stochastic processes.

Consider the expectation of the absolute error at the *final* time T of the Euler-Maruyama scheme. It can be shown that there exist constants C > 0 and $\delta_0 > 0$ such that

$$\mathbb{E}\left[|X_T - \hat{X}_{t_n}|\right] \le C\delta^{\frac{1}{2}}$$

for any time discretisation with maximum step size $\delta \in (0, \delta_0)$. It is said that the approximating process \hat{X}_t converges in the strong sense with order $\frac{1}{2}$. This is similar to how approximations are evaluated in a deterministic ODE, only here expectations are taken, since X_T and \hat{X}_{t_n} are random variables. Compare with the Euler scheme for an ODE which has order of convergence 1. Sometimes a close *path-wise* approximation is not required, but only some function of the value at a given final time T, such as $\mathbb{E}[X_T]$, $\mathbb{E}[X_T^2]$ or generally $\mathbb{E}[g(X_T)]$. In this case there exist constants C > 0 and $\delta_0 > 0$ such that for any polynomial function g

$$\left| \left[\mathbb{E}[g(X_T)] - \mathbb{E}E[g(\hat{X}_{t_n})] \right] \right| \le C\delta^1$$

for any time discretisation with maximum step size $\delta \in (0, \delta_0)$. The approximating process \hat{X}_t is said to *converge in the weak sense* with order 1.

Probability density function for a Wiener process

Consider a stochastic process X_t defined by equation equation (2.10). The associated Fokker-Planck equation, which gives the time evolution of the probability density function $\mathbb{P}(x, t)$ is

$$\frac{\partial}{\partial t} \mathbb{P}(x,t) = -\frac{\partial}{\partial x} \left(\mu(x,t) \mathbb{P}(x,t) \right) + \frac{1}{2} \frac{\partial^2}{\partial x^2} \left(\sigma^2(x,t) \mathbb{P}(x,t) \right), \qquad (2.24)$$

subject to an initial distribution, $\mathbb{P}(x, 0) = \delta(x)$, where $\delta(x)$ is the Dirac distribution function.

For the very simple case of a Wiener process, $dX_t = \sigma dW_t$, the PDF satisfies the well know diffusion equation

$$\frac{\partial}{\partial t} \mathbb{P}(x,t) = \frac{1}{2} \sigma^2 \frac{\partial^2}{\partial x^2} \mathbb{P} P(x,t),$$

whose solution is

$$\mathbb{P}(x,t) = \frac{1}{\sqrt{2\pi\sigma^2 t}} \exp\left(-\frac{x^2}{2\sigma^2 t}\right)$$

The solution represents the probability density function of a Normal distribution with mean zero and variance $\sigma^2 t$.

CHAPTER 3

Population dynamics in a simple stochastic environment

Introduction

The origins of population growth models are traced back to the influential Malthus' exponential model and later to Verhulst's logistic model [6]. 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 [36]. The logistic equation is

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K}\right),\tag{3.1}$$

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 [37] summarise some of these adaptations.

The carrying capacity is assumed to be constant in population growth models used for resource assessment and management [38]. However, changes to the carrying capacity do occur due to both exogenic and endogenic processes [9]. Long ago, Cushing [39] and Coleman [40] 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 [41].

The simplest approach is to specify some time-dependent function for the carrying capacity that reflects the observed behaviour of the changing environment [6, 26]. 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 con-

summers of those resources" [4]. To mitigate this issue, Safuan et al. [25, 26, 27, 28] developed models that treat the carry 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, contamination of water resources etc, that also need to be accounted for. By adding stochasticity (noise), 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 [42]. More generally environmental fluctuations are modelled by adding noise to the competition term (reciprocal of K) leading to the stochastic differential equation (SDE) [43];

$$dN_t = rN_t \left(1 - \frac{N_t}{K}\right) dt + r\sigma N_t^2 \, dW_t,\tag{3.2}$$

where W_t is a standard Weiner process with mean $\mathbb{E}[W_t] = 0$ and variance $\mathbb{V}[W_t] = t$. The noise intensity is σ . In the next section, a different approach is proposed, that the carrying capacity as a state-variable.



Figure 3.1: Three different realisations of K_t with $K_0 = 10$ and $\sigma = 0.4$.

The model

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

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K_t}\right), \qquad N_{t=0} = N_0 \qquad (3.3a)$$

$$dK_t = \sigma dW_t, \qquad \qquad K_{t=0} = K_0 \qquad (3.3b)$$

Equation (3.3a) is just the standard logistic differential equation as seen in equation (3.1) which describes the growth of a population as it responds to the fluctuations of the carrying capacity (K_t) . Equation (3.3b) defines the carrying capacity by a simple SDE, where σ is the intensity of the noise. Equation (3.3b) is solved independently from equation (3.3a), the solution is;

$$K_t = K_0 + \sigma W_t. \tag{3.4}$$

Substituting equation (3.4) into equation (3.3a), we get

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K_0 + \sigma W_t}\right). \tag{3.5}$$

Three different realisations (simulations) of equation (3.4) are shown in Figure (3.1). 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 . 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 (3.1) shows a realisation (green) that is a result of successive periods of below average rainfall leading to a deterioration of the carrying capacity: the ecosystem is experiencing a drought. If $K_t = 0$, then the environment can not sustain a population, leading to the population's extinction. Predicting extinction times and its causes is very important for conservation [44].

Expected population size

An exact solution to equation (3.5) 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 defined in equation (3.3) using the Euler-Maruyama method. Higham [35] described the 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 for K_t and N_t . For these cases 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. A step size of 0.01 seemed a reasonable compromise.



Figure 3.2: The effect of varying r on the mean and variance of the population with $K_0 = 10$, $\sigma = 0.1$ and $N_0 = 2$. In the top panel r = 0.2 and for the bottom panel r = 2.

Since $W_t \sim \mathsf{N}(0,t)$ and as K_t is a linear transformation of W_t , $K_t \sim \mathsf{N}(K_0, \sigma^2 t)$. From an ecological perspective this distribution is technically not correct as $K_t > 0$. It is possible to calculate the exact (conditional) PDF for $K_t > 0$;

$$\mathbb{P}(K_t, t) = \frac{1}{\sigma\sqrt{2\pi t}} \left[\exp\left(-\frac{(K_t - K_0)^2}{2\sigma^2 t}\right) - \exp\left(-\frac{(K_t + K_0)^2}{2\sigma^2 t}\right) \right].$$
 (3.6)

It is to be noted that the full PDF is the sum of a mass density function for the probability that $K_t = 0$ and the above PDF for $K_t > 0$. Here we are only concerned with the properties of equation (3.6). From equation (3.6) the mean, $\mathbb{E}[K_t]$, can be found as;

$$\mathbb{E}\left[K_{t}\right] = \int_{0}^{\infty} K_{t} \cdot \mathbb{P}\left(K_{t}, t\right) dK_{t}$$

$$= \int_{0}^{\infty} \frac{K_{t}}{\sigma\sqrt{2\pi t}} \cdot \left[\exp\left(-\frac{(K_{t} - K_{0})^{2}}{2\sigma^{2}t}\right) - \exp\left(-\frac{(K_{t} + K_{0})^{2}}{2\sigma^{2}t}\right)\right] dK_{t}$$

$$= \left\{\frac{K_{0}}{2} \cdot \left[\operatorname{erf}\left(\frac{K_{t} - K_{0}}{\sqrt{2\sigma^{2}t}}\right) + \operatorname{erf}\left(\frac{K_{t} + K_{0}}{\sqrt{2\sigma^{2}t}}\right)\right]$$

$$+ \frac{\exp\left(-\frac{(K_{t} - K_{0})^{2}}{2\sigma^{2}t}\right) - \exp\left(-\frac{(K_{t} + K_{0})^{2}}{2\sigma^{2}t}\right)}{\sqrt{2\pi}}\Big|_{0}^{\infty}$$
(3.7)

 $\mathbb{E}[K_t] = K_0$

where $\operatorname{erf}(x)$ is the Error function. From equation (3.7) it can be seen that the absorbing boundary, $K_t = 0$, does not change the value of the mean of the carrying capacity; $\mathbb{E}[K_t]$. In a similar way, the variance of the carrying capacity can be found to be;

$$\begin{aligned} \mathbf{\nabla} \left[K_t \right] &= \mathbf{\mathbb{E}} \left[\left(K_t \right)^2 \right] - \left(\mathbf{\mathbb{E}} \left[K_t \right] \right)^2 = \int_0^\infty \left(K_t \right)^2 \cdot \mathbf{\mathbb{P}} \left(K_t, t \right) dK_t - K_0^2 \right) \\ \mathbf{\mathbb{E}} \left[\left(K_t \right)^2 \right] &= \int_0^\infty \frac{\left(K_t \right)^2}{\sigma \sqrt{2\pi t}} \cdot \left[\exp\left(-\frac{\left(K_t - K_0 \right)^2}{2\sigma^2 t} \right) - \exp\left(-\frac{\left(K_t + K_0 \right)^2}{2\sigma^2 t} \right) \right] dK_t \\ &= \left\{ \frac{\sigma^2 t + K_0^2}{2} \cdot \left[\operatorname{erf} \left(\frac{K_t - K_0}{\sqrt{2\sigma^2 t}} \right) + \operatorname{erf} \left(\frac{K_t + K_0}{\sqrt{2\sigma^2 t}} \right) \right] \\ &- \frac{\sigma \sqrt{t}}{\sqrt{2\pi}} \cdot \exp\left(-\frac{\left(K_t + K_0 \right)^2}{2\sigma^2 t} \right) \cdot \left[\left(K_t + K_0 \right) \cdot \exp\left(\frac{2K_0 K_t}{\sigma^2 t} \right) - K_t + K_0 \right] \right]_0^\infty \\ &= \left(\sigma^2 t + K_0^2 \right) \cdot \operatorname{erf} \left(\frac{K_0}{\sqrt{2\sigma^2 t}} \right) + \frac{K_0 \sqrt{2\sigma^2 t}}{\sqrt{\pi}} \cdot \exp\left(-\frac{K_0^2}{2\sigma^2 t} \right) \end{aligned}$$
(3.8)

In equation (3.8) it is obvious that the variance of the carrying capacity, $\mathbf{V}[K_t]$, with an absorbing boundary, $(K_t = 0)$, is very different to the variance without an absorbing barrier, $\mathbf{V}[W_t] = \sigma^2 t$. For small values of t, it can be seen that the variance, $\mathbf{V}[K_{t\approx 0}] \approx \sigma^2 t$, is linear and for large values of time it can be seen that the variance, $\mathbf{V}[K_{t\approx 0}] \approx \frac{K_0 \sqrt{2\sigma^2 t}}{\sqrt{\pi}} - K_0^2$, is proportional to the \sqrt{t} .

Since N_t pursues K_t , this suggests that the population has (asymptotically) a similar distribution to that of the carrying capacity: $P_N(N,t|N_0) \approx P_K(K,t|K_0)$. To investigate this a Monte Carlo approach was employed and the mean and variance of 2000 simulations were calculated. Figure (3.2) supports the idea that the population has a mean and variance that closely matches the mean and variance of the carrying capacity. An interesting point to note is that a smaller value of r does not affect the mean asymptotically approaching K_0 , but does slightly reduce the variance.

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 . 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 (3.3) 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. When interpreting the qq-plots the closer the quantiles lie to a straight line, the more likely they belong to the same distribution. For the different times and σ , the distributions of N_t and K_t are likely to be the same.

Using qq-plots, Figure (3.4) 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 straight line. For small enough σ and large enough K_0 the second term in equation (3.6) is small and the assumption of normality holds true for a restricted amount of time.

When $\sigma = 0.4$, as time increases, the tails of the qq-plot becomes noticeably less linear, especially on left. 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 equation (3.6), which gives $\mathbb{P}_K(0, t|K_0) = 0$.



Figure 3.3: The qq-plots of distributions for K_t and N_t with $K_0 = 10$, r = 0.2 and $N_0 = 2$.



Figure 3.4: The qq-plots showing if the distributions K_t and N_t are normally distributed, with $K_0 = 10$, r = 0.2 and $N_0 = 2$.

Distribution of extinction times

Recall that $K_t = K_0 + \sigma W_t$ is a scaled Wiener process with mean K_0 . The firsthitting time when the carrying capacity reaches zero, $\tau = \inf\{t : K_t = 0\}$, 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 given by [30],

$$f_{\tau}(t) = \frac{K_0}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{K_0^2}{2\sigma^2 t}\right).$$
(3.9)

Figure (3.5) 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 equation (3.9). Furthermore, extensive numerical simulations indicated that the first-hitting times for N_t may be approximated by those for K_t .



Figure 3.5: 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 $\sigma = 0.1$.

Chapter 4

Environment as an Ornstein-Uhlenbeck process

Introduction

Verhulst's well know logistic model includes the concept of a 'saturation level' or carrying capacity, a value that represents the maximum population that an environment can sustain [36]. The logistic equation is written as

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K}\right),\tag{4.1}$$

where N_t is the population at time t, r is the intrinsic growth rate and K is the carrying capacity.

This simple model has been adapted for over a century, [37]. The carrying capacity, often assumed to be a constant [38], can change due to exogenic and endogenic processes [9]. Models where the carrying capacity is treated as a function of time to describe changing environmental conditions can be found in Cushing [39] and Coleman [40].

The simplest approach to modelling a changing environment is by specifying the carrying capacity as a time-dependent function [26]. However, this approach is limiting, as it does not allow for the environment to be shaped by the interdependent relationships between the resources and the population that consumes them [4]. This issue was mitigated in a series of papers, Safuan et al. [23, 25, 27, 28], models were developed that treated the carrying capacity as a state-variable coupled to the population model.

The variations to the logistic model mentioned thus far have their applications, however, there are many external environmental factors like; fire, drought, floods, resource contamination, etc that need to be accounted for. By adding stochasticity to the model, it is possible to account for the effects of such perturbations on the population that deterministic models ignore. How stochasticity is added to population models is a modelling issue. Usually, environmental fluctuations are modelled by adding noise to the 'crowding term' (the reciprocal of the carrying capacity), the nonlinear term of equation (4.1), leading to [32, 43],

$$dN_t = rN_t \left(1 - \frac{N_t}{K}\right) dt + r\sigma N_t^2 dW_t.$$
(4.2)

Here W_t is a standard Weiner process with $\mathbb{E}[W_t] = 0$, $\mathbb{V}[W_t] = t$ and the noise intensity is σ .

The model

An alternate approach was proposed by Safuan et al. [23]. The approach is based on treating the carrying capacity as a state variable, that is, governed by a separate equation that describes the changes in the carrying capacity. A simple stochastic extension of the Safuan et al. [23] model is

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K_t}\right), \qquad \qquad N_{t=0} = N_0 \qquad (4.3a)$$

$$dK_t = -\gamma (K_t - k_1) dt + \sigma dW_t, \qquad K_{t=0} = K_0$$
 (4.3b)

The population, N_t , is still modelled by a logistic equation but now coupled to the carrying capacity, K_t , which in turn is modelled by a stochastic differential equation. Equation (4.3b) consists of a deterministic and a stochastic term. In the absence of random variations, $\sigma = 0$, equation (4.3) can be solved exactly [26]. It represents a model for the growth of bacteria under an occlusion of the skin.

Equation (4.3b) is commonly known as the Ornstein-Uhlenbeck (OU) equation, a stochastic process that is stationary, Markovian and Gaussian [45]. The OU equation is 'mean-reverting' (drifts towards its long-term mean k_1). Figure (4.1) shows several realisations (paths or trajectories) of K_t with with different parameters. From the top plot the 'mean reverting' nature of the OU equation can be seen: starting with different initial conditions K_0 all realisations approach k_1 . How fast realisations of K_t approach k_1 depends on γ . It places a constraint on how large the random variations can get. Large variations, either above or below k_1 are pulled back to k_1 . The bottom plot shows realisation of K_t for different noise intensities, $\sigma = 1$, 0.5, 0.1. In particular it depicts a realisation that reaches $K_t = 0$ in finite time when σ is large, in a relative sense to other parameters. If the situation arises such that $K_t = 0$, then the environment can no longer sustain the population leading to extinction. From a conservationist perspective, predicting extinction times are very important [44]. As equation (4.3b) is independent of N_t it can be solved separately, giving the well known solution of the OU equation

$$K_t = k_1 + (K_0 - k_1) e^{(-\gamma t)} + \sigma \int_0^t e^{\gamma(s-t)} dW_s.$$
(4.4)

Substituting equation (4.4) into equation (4.3a) leads to

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{k_1 + (K_0 - k_1) e^{(-\gamma t)} + \sigma \int_0^t e^{\gamma(s-t)} dW_s} \right), \quad N_{t=0} = N_0. \quad (4.5)$$

The exact solution of equation (4.5) is currently unknown, the numerical solution is discussed in the next section.



Figure 4.1: Three different realisations of K_t with parameters (top) $\gamma = 0.03$ and $\sigma = 0.1$, (bottom) $K_0 = 15$ and $\gamma = 0.01$. For both cases $k_1 = 10$.

Expected solution path

According to equation (4.4), the distribution of K_t (conditioned on K_0) is normal, $K_t \sim N(\mu_t, \sigma_t^2)$, with (conditional) mean and variance

$$\mu_t = \mathbb{E}[K_t] = k_1 + (K_0 - k_1) e^{-\gamma t}, \qquad (4.6)$$

$$\sigma_t^2 = \mathbf{V}(K_t) = \frac{\sigma^2}{2\gamma} \left(1 - e^{-2\gamma t} \right).$$
(4.7)

However, from an ecological perspective, we require that $K_t > 0$, therefore the exact conditional probability distribution for $K_t > 0$ is [46]

$$\mathbb{P}(K_t, t|K_0) = \frac{1}{\sqrt{2\pi\sigma_t^2}} \left[\exp\left(-\frac{(K_t - \mu_t)^2}{2\sigma_t^2}\right) - \exp\left(-\frac{(K_t + \mu_t)^2}{2\sigma_t^2}\right) \right].$$
(4.8)

Note that $\mathbb{P}(K_t = 0, t | K_0) = 0$ constitutes the absorbing boundary condition; when the carrying capacity reaches zero it remains there. Ecologically this later condition represents the collapse of the environment thus leading to the extinction of the population. Similar to that of the Wiener process discussed on page 27, the exact PDF consists of the sum of a mass density function at $K_t = 0$ and equation (4.8).

Knowing the properties of K_t , a Monte Carlo approach was employed to determine the distribution of N_t as well as its mean and variance. This was achieved by constructing 40,000 realisations of equation (4.4). For each realisation, equation (4.5) was solved numerically using Euler's method with a step size of $\Delta t = 0.01$. This size of Δt was a good compromise between accuracy and computational effort. The mean and variance of K_t and N_t are plotted in Figure (4.2).

On both plots, the simulated K_t is plotted in black, the simulated N_t is plotted in blue, for the initial conditions $K_0 = 15$ and $N_0 = 2$. The top plot shows the (conditional) mean of K_t which coincides with the predicted mean given by equation (4.6). It is possible to write the solution to equation (4.5) formally as

$$N_t = \frac{e^{rt}}{\frac{1}{N_0} + \int_0^t \frac{re^{rs}}{K_s} ds}.$$
(4.9)

An exact algebraic expression for $\mathbb{E}[N_t]$ is not possible. An approximate expression



Figure 4.2: The mean and variance of the carrying capacity and the population. The plot shows both the numerically simulated values and the analytical model. Here $K_0 = 15$, $k_1 = 10$, $N_0 = 2$, r = 0.1, $\gamma = 0.05$ and $\sigma = 0.5$.

for the (conditional) mean of N_t is

$$\mathbb{E}\left[N_t\right] \approx \frac{e^{rt}}{\frac{1}{N_0} + \int_0^t \frac{re^{r\mu}}{\mathbb{E}\left[K_\mu\right]} d\mu},\tag{4.10}$$

The predicted mean for N_t is also shown in the plot (red). Apart from the early transient behaviour the means of K_t and N_t both approach k_1 , independent of the initial conditions.

Similarly, in the bottom plot, the (conditional) variance of K_t matches up with the theoretical expression given by equation (4.7). No simple expression for the variance of N_t could be found. We note that $\mathbf{V}(N_t) < \mathbf{V}(K_t)$ for all time t. However, beyond some time, $t \gg 1/\gamma$, each asymptotically converges to some constant, but different, value.

A quantile-quantile plot (qq-plot) of the simulated values of N_t against K_t is shown in Figure (4.3). It demonstrates that the distributions are similar and since the slope of the line is less than one it further indicates that $\mathbf{V}(N_t) < \mathbf{V}(K_t)$, as mentioned previously.



Figure 4.3: Quantile-quantile plots at different times of the population (N_t) against the carrying capacity (K_t) . The parameters are: $K_0 = 15$, $N_0 = 5$, $k_1 = 10$, r = 0.1, $\gamma = 0.05$ and $\sigma = 0.1$.

Distribution of extinction times

As alluded to previously we require $K_t > 0$ for all t. However as can be seen from Figure (4.1) there is a realisation for which K_t reaches zero. For fixed k_1 and K_0 , according to (4) this is possible depending on the relative size of γ and σ . On the characteristic time scale of $1/\gamma$ the dynamics of K_t is predominantly governed by the Weiner process, W(t), and if σ is large then it is possible for K_t to reach zero. The instant $K_t = 0$, it remains there and the environment has collapsed; which leads to the subsequent extinction of the population. The probability of the environment collapsing by a given time t, is $1 - S(t|K_0)$, where $S(t|K_0)$ is the survival function,

$$S(t|K_0) = \int_0^\infty \mathbb{P}(K_t, t|K_0) \, dK_t$$

The distribution of the first-hitting (extinction) time represents the probability density for which K_t has collapsed by time t. It is defined by $f(t|K_0) = -S'(t|K_0)$. The distribution is [47]



Figure 4.4: Plot showing both the theoretical and numerical probability distribution function of the first-hitting time for K_t with $K_0 = 12$, $k_1 = 10$, r = 0.5, $\gamma = 0.01$ and $\sigma = 2$.

$$f(t) = \frac{2 \exp\left(-\frac{\mu_t^2}{2\sigma_t^2}\right)}{\sqrt{2\pi\sigma_t^2}} \cdot \left(\frac{\mu_t \sigma_t'}{\sigma_t} - \mu_t'\right)$$
(4.11)

where μ_t and σ_t^2 are given by equation (4.6) and equation (4.7), respectively. Here, μ'_t and σ'_t are the derivatives of the mean and variance. Figure (4.4) is a plot of the probability density function for the first-hitting times. The Monte Carlo simulations are shown as dots (blue) and the line is the theoretical probability density function given by equation (4.11). It is clear that equation (4.11) is a good approximation. Furthermore, extensive numerical simulations indicated that the first-passage times for N_t may also be approximated by those of K_t .

CHAPTER 5

Conclusion

This final Chapter provides concluding remarks as well as some suggested extensions that stem directly result from the models described in the thesis.

Concluding remarks

Physical environments are rarely static. It is well recognised that environmental parameters such as temperature and rainfall have strong impacts on natural populations of plants and animals. This thesis provides an analysis of a simple ecosystem comprising of a single-species population inhabiting an environment that is subject to random fluctuations. A logistic differential equation is used to model the dynamics of the population while treating the carrying capacity, a proxy variable for the state of the environment, as a state-variable. This approach differs from current approaches and interpretations.

Two different stochastic process for the carrying capacity are considered. The first is a Wiener process with a non-zero mean. This model for the environment is not terribly realistic, however a possible interpretation based on deviations from say, average monthly rainfall over a region, is still meaningful. The second is an OU process. This process may find application for the growth of bacteria under an occlusion of the skin [23, 26].

To describe the probabilistic nature of the environment, the exact PDF for both processes was derived. An exact treatment of the population size is not possible. Numerical simulations based on a Monte-Carlo approximation show that the population N_t 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. Figure (5.1) where the carrying capacity is modelled as a Wiener process illustrates the effect of varying the intrinsic growth rate (r). Similar behaviour is also obtained for the OU process.



Figure 5.1: Evolution of the population for two different growth rates. Here $N_0 = 2$, $K_0 = 10$, $\sigma = 0.5$ and $\Delta t = 0.01$.

For the Wiener model, simulations demonstrate that for small σ and large K_0 the distribution for K_t was approximately normal. Since $K_t > 0$ the distribution is certainly not normal. Both K_t and N_t are better approximated by a skewed distribution. Moreover, simulations for the OU process, reveal that for small σ and large N_0 , K_0 and k_1 the distribution of K_t is approximately normal even when $K_t > 0$. The qq-plots indicated that N_t has a similar distribution to K_t , thus the distribution of N_t is also approximately normal. Beyond the early transient period, the means are the same and the variance is constant, albeit smaller for N_t .

These observations can be explained with reference to logistic differential equation. No matter how complicated the carrying capacity appears as long as it is independent of N_t then in principle it can be solved for K_t . From the differential equation for N_t , when K_t is higher than N_t , N_t will increase toward K_t and when K_t is lower it will decrease toward K_t . This implies that the population N_t will always pursue the carrying capacity K_t . In the special case where r is large this means that the rate of change of N_t will be large in magnitude so that it follows K_t more closely. For this reason, the fluctuations of N_t will always be smaller than K_t , $\mathbf{V}(N_t) < \mathbf{V}(K_t)$. In the extreme case where $r \to \infty$ then $N_t = K_t$, so that the distribution of N_t will be the same as the distribution of K_t . In this case only does $\mathbf{V}[N_t] = \mathbb{E}[K_t]$.

To formally show this, start with the coupled SDE

$$\frac{dN_t}{dt} = rN_t \left(1 - \frac{N_t}{K_t}\right), \qquad N_{t=0} = N_0 \qquad (5.1a)$$

$$dK_t = \sigma dW_t, \qquad \qquad K_{t=0} = K_0 \qquad (5.1b)$$

where $\sigma > 0$ is the intensity of the noise. Recall the solution for K_t is $K_t = K_0 + \sigma W_t$, which implies $K_t \sim N(K_0, \sigma^2 t)$. The solution to the differential equation for N_t is

$$N_t = \frac{N_0}{e^{-rt} + N_0 \int_0^t \frac{re^{-r(t-s)}}{K_s} ds}, \quad t > s.$$
(5.2)

Consider,

$$\lim_{r \to \infty} N_t = \lim_{r \to \infty} \frac{N_0}{e^{-rt} + N_0 \int_0^t \frac{r e^{-r(t-s)}}{K_s} ds}.$$
(5.3)

The first term in the denominator is zero, to evaluate the second term we note,

$$\lim_{r \to \infty} r e^{-r(t-s)} = \delta(t-s), \quad t > s, \tag{5.4}$$

where $\delta(t-s)$ is the Dirac delta function. Then

$$\lim_{r \to \infty} \int_0^t \frac{r e^{-r(t-s)}}{K_s} ds = \int_0^t \frac{\delta(t-s)}{K_s} ds, \quad t > s,$$
(5.5)
$$= \frac{1}{K_t},$$

leading to

$$\lim_{r \to \infty} N_t = K_t. \tag{5.6}$$

The practical implication is that for large values of the intrinsic birth rate, r, the distributions for N_t and K_t are approximately the same. What the situation is for the more realistic and interesting case, small r, is beyond the scope of this thesis.

The next step is to construct and numerically solve the Fokker-Planck equation for the joint PDF of N_t and K_t including the appropriate absorbing boundary conditions for N_t and K_t . The marginal distributions can then be calculated from which estimates of extinction times can be determined [44]. This latter knowledge is important in the consideration of possible conservation practices. The analysis is beyond the scope of this thesis.

Future work

A few possible extensions are offered.

Environmental stochasticity: a modelling issue

Changes in environmental conditions also leads to a response in the species' fecundity, thus modelling the growth rate r_t with noise as well as the carrying capacity K_t is an important extension.

Using a multiplicative noise to model the effect of stochastic fluctuations in the intrinsic growth rate and for the carrying capacity being represented by a Wiener process, we get

$$dN_t = rN_t \left(1 - \frac{N_t}{K_t}\right) dt + \sigma_1 N_t \ dW_t^{(1)}, \qquad N_{t=0} = N_0$$
(5.7a)

$$dK_t = \sigma_2 dW_t^{(2)}, \qquad K_{t=0} = K_0 \qquad (5.7b)$$

where $W_t^{(1)}$ and $W_t^{(2)}$ are standard and uncorrelated Wiener processes. This model can be modified to account for a degree of correlation by writing

$$dN_t = rN_t \left(1 - \frac{N_t}{K_t}\right) dt + N_t \left(\sigma_1 \rho \ dW_t^{(1)} + \sigma_2 \sqrt{1 - \rho^2} \ dW_t^{(2)}\right)$$
(5.8a)

$$dK_t = \sigma_1 \sqrt{1 - \rho^2} \ dW_t^{(1)} + \sigma_2 \rho \ dW_t^{(2)}$$
(5.8b)

where $|\rho| \leq 1$ may be thought of as a correlation parameter. The additional aim is to understand the effect of ρ on population dynamics.

Gompertz model

Another equally popular model is the Gompertz differential equation

$$\frac{dN_t}{dt} = \gamma N_t \left(\ln(K) - \ln(N_t) \right), \tag{5.9}$$

where K has the meaning of carrying capacity, similar to that of the logistic differential equation, and γ is a parameter.

Originally, the Gompertz model was not written as equation (5.9). It was motivated by seeking a model with non-constant human mortality rates, being expressed as a decaying function with time, namely

$$\frac{dN_t}{dt} = rN_t, \quad \text{with } r = a_0 e^{-\gamma t}, \tag{5.10}$$

where a_0 is the maximal growth rate. To see how the carrying capacity emerges note that on separating variables and integrating

$$\ln(N_t) = -\frac{a_0}{\gamma}e^{-\gamma t} + C$$

where C is an arbitrary constant of integration. Now assuming that as $t \to \infty$, $N_t \to K$, leads to

$$\ln\left(\frac{N_t}{K}\right) = -\frac{a_0}{\gamma}e^{-\gamma t}$$

then substitution into equation (5.10) leads to equation (5.9). Thus introducing the carrying capacity, a purely mathematical outcome.

More fundamental, however, is to treat the growth rate as a state-variable

$$\frac{dr}{dt} = -\gamma r, \quad r(0) = a_0. \tag{5.11}$$

In the deterministic cases all three representations of the Gompertz differential equation are equivalent. What is not clear is if this is true for their stochastic versions. Since stochasticity enters the model via γ , how noise appears in equation (5.9) and equation (5.11) is quite different. It is not certain that the concept of a carry capacity has any meaning in this case.

The carrying capacity as a potential

Suppose that the state-variable is now described by the equation

$$\frac{dK_t}{dt} = -\frac{d\nu(K_t)}{dK_t} + \xi_t$$

where $\nu(K_t) > 0$ (for all $K_t > 0$) is a quartic bistable potential with two local minima, $K_a < K_b$ such that $\nu(K_a) < \nu(K_b)$. Define $h = \nu(K_b) - \nu(K_a) \ge 0$. When h = 0 the potential is symmetric. For this situation and under stochastic perturbation an important consideration is to estimate the mean waiting-time before the environment 'escapes' the state K_b and accelerates towards the new equilibrium state K_a . If h = 0 or $h \ne 0$ (but still small), it might be possible for the ecosystem to transition back to the higher state after some mean waiting-time in state K_a . If on the other hand h is very much larger than the noise intensity, the environment with a lower carrying capacity may become the new permanent state.

Such a situation may have significant consequences for a native population. A more hostile environment would reduce the population size thus making it more vulnerable to other types of environmental stresses, including predation by invasive species.

This approach may contribute to the important area of catastrophic ecological regime shift that is claimed to be the mechanism for the sudden extinction of species.

Bibliography

- D. A. Jillson. Insect populations respond to fluctuating environments. *Nature*, 288:699–700, 1980.
- [2] S. Chapman, K. Mustin, A. R. Renwick, D. B. Segan, D. G. Hole, R. G. Pearson, and J. E. M. Watson. Publishing trends on climate change vulnerability in the conservation literature reveal a predominant focus on direct impacts and long time-scales. *Diversity and Distributions*, 20:1221–1228, 2014.
- [3] T. Malthus. An essay on the principle of population, as it affects the future improvement of society with remarks on the speculations of Mr. Godwin, Mr. Condorcet, and other writers. *St. Pauls Churchyard, London*, 1798.
- [4] P. del Monte-Luna, B. W. Brook, M. J. Zetina-Rejón, and V. H. Cruz-Escalona. The carrying capacity of ecosystems. *Global Ecology and Biogeography*, 13:485–495, 2004.
- [5] P. F. Verhulst. Notice sur la loi que la population poursuit dans son accroissement. *Correspondance mathematique et physique*, 10:113–121, 1838.
- [6] R. B. Banks. Growth and Diffusion Phenomena. Springer-Verlag, Berlin, 1994.
- [7] R. Pearl and L. J. Reed. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of* the National Academy of Sciences of the United States of America, 6:275–288, 1920.
- [8] J. Vandermeer. The competitive structure of communities: an experimental approach with protozoa. *Ecology*, 50:362–371, 1969.
- [9] J. E. Cohen. Population growth and earth's human carrying capacity. Science, 269:341–346, 1995.
- [10] P. E. Waggoner. How much land can ten billion people spare for nature? Daedalus, 125:73–93, 1996.
- [11] P. S. Meyer and J. H. Ausubel. Carrying capacity: A model with logistically varying limits. *Technological Forecasting and Social Change*, 61:209–214, 1999.
- [12] D. Ludwig, R. Hilborn, and C. Walters. Uncertainty, resource exploitation, and conservation: lessons from history. *Science*, 260:17–36, 1993.
- [13] J. S. Jones. Of cannibals and kin. Nature, 299:202–203, 1982.
- [14] R. F. Costantino, J. M. Cushing, B. Dennis, R. A. Desharnais, and S. M. Henson. Resonant population cycles in temporally fluctuating habitats. *Bulletin* of Mathematical Biology, 60:247–273, 1998.

- [15] B. D. Coleman, Y. Hsieh, and G. P. Knowles. On the optimal choice of r for a population in a periodic environment. *Math. Biosci.*, 46:71–85, 1979.
- [16] J. M. Cushing. Oscillatory population growth in periodic environments. Theoretical Population Biology, 30:289–308, 1986.
- [17] S. P. Rogovchenko and Y. V. Rogovchenko. Effect of periodic environmental fluctuations on the Pearl-Verhulst model. *Chaos, Solitons & Fractals*, 39:1169– 1181, 2009.
- [18] M. Aluja, H. Celedonio-Hurtado, P. Liedo, M. Cabrera, F. Castillo, J. Guillén, and E. Rios. Seasonal population fluctuations and ecological implications for management of Anastrepha fruit flies (Diptera: Tephritidae) in commercial mango orchards in Southern Mexico. *Journal of Economic Entomology*, 89: 654–667, 1996.
- [19] P. Turchin and S. P. Ellner. Living on the edge of chaos: population dynamics of Fennoscandian voles. *Ecology*, 81:3099–3116, 2000.
- [20] T. Grozdanovski, J. J. Shepherd, and A. Stacey. Multi-scaling analysis of a logistic model with slowly varying coefficients. *Applied Mathematics Letters*, 22:1091–1095, 2009.
- [21] J. J. Shepherd and L. Stojkov. The logistic population model with slowly varying carrying capacity. *ANZIAM Journal*, 47:492–506, 2007.
- [22] S. Ikeda and T. Yokoi. Fish population dynamics under nutrient enrichment—a case of the East Seto Inland Sea. *Ecological Modelling*, 10:141–165, 1980.
- [23] H. M. Safuan, Z. Jovanoski, I. N. Towers, and H. S. Sidhu. A simple model for the total microbial biomass under occlusion of healthy skin. In 19th International Congress on Modelling and Simulation, pages 733–739, Perth, Australia, December 2011.
- [24] P. Meyer. Bi-logistic growth. Technological Forecasting and Social Change, 47: 89–102, 1994.
- [25] H. M. Safuan, Z. Jovanoski, I. N. Towers, and H. S. Sidhu. Coupled logistic carrying capacity model. ANZIAM J., 53:C172–C184, 2012.
- [26] H. M. Safuan, Z. Jovanoski, I. N. Towers, and H. S. Sidhu. Exact solution of a non-autonomous logistic population model. *Ecological Modelling*, 251:99–102, 2013.
- [27] H. M. Safuan, Z. Jovanoski, I. N. Towers, and H. S. Sidhu. Impacts of biotic resource enrichment on predator-prey population. *Bull. Math. Biol.*, 75:1798– 1812, 2013.
- [28] H. M. Safuan, Z. Jovanoski, I. N. Towers, and H. S. Sidhu. A two-species predator-prey model in an environment enriched by a biotic resource. ANZIAM J., 54:C768–C787, 2014.

- [29] R. Huzimura and T. Matsuyama. A mathematical model with a modified logistic approach for singly peaked population processes. *Theo. Pop. Bio.*, 56: 301–306, 1999.
- [30] C. W. Gardiner. Handbook of Stochastic Methods, 2nd ed. Springer-Verlag, Berlin, 1985.
- [31] S. M. Iacus. Simulations and Inference for Stochastic Differential Equations with R examples. Springer-Verlag, Berlin, 2008.
- [32] P. E. Kloeden and E. Platen. Numerical Solution of Stochastic Differential Equations. Springer-Verlag, Berlin, 1992.
- [33] F. B. Hanson. Applied stochastic processes and control for Jump-diffusions: modeling, analysis, and computation. Society for Industrial & Applied Mathematics, United States, 2007.
- [34] C. H. Edwards and D. E. Penny. Differential equations and boundary value problems: computing and modeling, 4th edition. Pearson, New Jersey, 2008.
- [35] D. J. Higham. An algorithmic introduction to numerical simulation of stochastic differential equations. SIAM. Review, 43:525–546, 2001.
- [36] F. Brauer and C. Catillo-Chàvez. Mathematical Models in Population Biology and Epidemiology. Springer, New York, 2001.
- [37] A. Tsoularis and J. Wallace. Analysis of logistic growth models. Math. Biosci, 179:21–55, 2002.
- [38] S. Oppel, H. Hilton, N. Ratcliffe, C. Fenton, J. Daley, G. Gray, Vickery J., and D. Gibbons. Assessing population viability while accounting for demographic and environmental uncertainty. *Ecology*, 95:1809–1818, 2014.
- [39] J. M. Cushing. Periodic time-dependent predator-prey systems. Siam J. Appl. Math., 32:82–95, 1977.
- [40] B. D. Coleman. Nonautonomous logistic equation as models of the adjustment of populations to environmental change. *Math. Biosci.*, 45:159–173, 1979.
- [41] J. Vandermeer. Seasonal ioschronic forcing of lotka volterra equations. Progress of Theoretical Physics, 96:13–28, 1996.
- [42] S. M. Hensom and J. M. Cushing. The effect of periodic habitat fluctuations on a nonlinear insect population model. J. Mathematical Biology, 36:201–226, 1997.
- [43] V. Méndez, I. Liopis, D. Campos, and W. Horsthemke. Extinction conditions for isolated populations affected environmental stochasticity. *Theoretical Population Biology*, 77:250–256, 2010.
- [44] P. Foley. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology*, 8:124–137, 1994.

- [45] G. E. Uhlenbeck and L. S. Ornstein. On the theory of brownian motion. Phys. Rev., 36:823–841, 1930.
- [46] W. Feller. An Introduction to Probability Theory and Its Applications. Wiley Series in Probability and Mathematical Statistics, Vol II. John Wiley and Sons, Inc, New York, 1996. Page 341.
- [47] M. C. Wang and G. E. Uhlenbeck. On the theory of the brownian motion ii. *Review of Modern Physics*, 17:323–342, 1945.