Persistence of managed populations: simple models and an application to the Islay barnacle goose population

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Contents

I. Persistence in simple stochastic population models 12

II: Persistence time applied in assessing management of the Islay wintering barnacle geese 135

Chapter 6: Barnacle geese on Islay: population status and agricultural conflicts 136

Chapter 7: An assessment of shooting as a tool in the management of the Islay barnacle geese 165

Abstract

Persistence time is introduced as a measure of the viability of a population described by a stochastic model of particular applicability when management decisions must be made on the basis of available data.

Various results for the first passage time of simple stochastic processes are presented which can provide persistence time estimates in population modelling. This area of the literature is found to be rather undeveloped and accurate results are not widely available.

Application of results for the Wiener process provides a complete set of approximations to the problem of persistence time in population models with density and serially independent vital rates. The properties of persistence time in such models are investigated and various ecological implications considered.

A linear model with a hard upper bound to population size is introduced which prevents populations growing to unrealistic sizes. Persistence time results applied to data for the acorn woodpecker with a limited number of territories. Immigration and/or density dependent vital rates are likely to be operating to account for observed persistence.

Persistence time in density dependent models where the population is regulated around some mean level is found to be exponentially distributed except at short times. Two methods are used to provide insight, but results in this area are generally lacking.

The data relating to barnacle geese wintering on Islay is analysed. The growing population has come into increasing conflict with agriculture. Persistence time is used as a viability measure in the investigation of management strategies involving controlled shooting. While some of these strategies could successfully regulate the population without greatly affecting likely persistence time, current UK and EC legislation would make applying these methods difficult. New compensation measures may reduce the conflict at present, but if natural population regulation is not seen to take effect this conflict is likely to return.

Acknowledgements

I am grateful to many people who, in various ways, have contributed to this work. Roger Nisbet, my first supervisor at Strathclyde, managed to channel my unspecific interest in mathematical ecology in useful directions, providing much of the initial direction to this work and being a constant source of ideas ever since. He also provided balanced advice as this thesis came together despite the problems of transporting documents successfully round the globe. Bill Gurney had the unenviable task of supervising the later stages of this work, helping face some of the problems of persistence time in non-linear models, and encouraging me to finish. I have also learnt much from his computer code ! Other members of the Department of Statistics and Modelling Science have provided help on several occasions: I am particularly grateful to Roy Veich who, apart from managing the computing resources on which I rely, provided a rigorous treatment of the mathematics of the Wiener process with an absorbing and reflecting barrier. His assistance finally cleared away much confusion and enabled chapter 4 of this thesis to come about.

Much of the initial impetus for the application of modelling to the problem of managing the Islay wintering barnacle goose population came from Sandy Kerr. For advice and discussions on the goose related work I am grateful to Ralph Kirkwood, David Houston, George Jackson, Ron MacDonald, Mike Peacock, Malcolm Ogilvie, Myrfen Owen, and, in particular, Steve Percival and Tony Fox.

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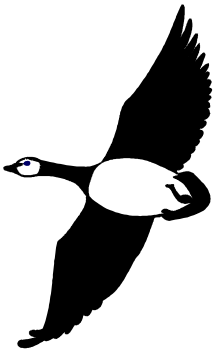
Persistence, avoidance of extinction, is at the root of the most fundamental questions of ecology.

Strong (1990)



Chapter 1

Introduction

Many areas of ecology ask questions about the persistence of species, population and communities: if, and why, they persist, and for how long. Persistence is also one of the major issues involved when the science of ecology meets the "real world" on the issue of conservation. This thesis is concerned with one particular aspect of ecological persistence: the time for which population size, in particular the size of managed populations, persists above some threshold number of individuals. The question of how different population management strategies change the likely persistence time is a central issue in applying these results.

Background and layout of the thesis

The work reported here grew from interest in a specific management problem, that of managing the population of barnacle geese which winters on the island of Islay, one of the Inner Hebrides off the west coast of Scotland. The conflict between conservationists (keen to see the barnacle goose population flourish) and farmers (concerned at losses from barnacle geese grazing on their land) led the then Nature Conservancy Council to approach R.M. Nisbet to produce models of the population consequences of shooting geese under various control regimes. This resulted in various deterministic models (Nisbet 1989, Middleton, Nisbet & Kerr 1993) but identified the need for stochastic models to account for the observed variation in the population numbers and vital rates. My work on these particular models makes up the second part of this thesis, following on from work of a more general nature that arose as a consequence of this problem.

During the investigation of these stochastic models for the Islay barnacle geese, it became apparent that there was a need for a viability measure that allowed the impact of various management strategies to be compared. This criterion that has been used here is the time that the population persists above some threshold. In the rest of this chapter this criterion is discussed in the context of models of managed populations.

For much of the initial work on the Islay barnacle geese models the persistence time was calculated numerically, a process that not only requires the use of considerable computing resources but yields relatively little insight into issues beyond the specific cases considered. Analytical approaches to the problem of persistence time are therefore highly desirable. Chapters three to five explore various analytical methods for describing persistence time in some simple population models. Chapter two lays the essential ground work by bringing together, in a common notation, a variety of results from the literature that provide much of the mathematical background for this work.

Modelling in species conservation and management

Those working in population management have to decide on appropriate strategies for the management of a species which reconcile, where possible, the conflicting demands of various interested parties. Decisions must often be made on the basis of less than optimal data on the population dynamics of the species in question. The fact that much conservation effort is directed toward a single population of a species does not leave a great deal of room for experimenting with different management strategies. In this situation modelling may provide some assistance. If, using the data available at the time when the management decisions have to be made, a model can be constructed that adequately represents the population dynamics of the species in question then it should be possible to experiment with various management strategies using the purely hypothetical replicate populations represented by the model.

A science of conservation biology has emerged in recent years, with quite an emphasis on applying general ecological theory, and modelling techniques (see, for example, papers in Soulé 1986,87 and Perrins, Lebreton & Hirons 1991). However academic conservation biology and actual conservation practice often have differing emphases. For instance, academic conservation research expended much energy on the question of whether it was better to have a single large reserve, or several small reserves totalling a similar area, (the 'SLOSS debate'), a question initially prompted by Diamond's (1975) application of MacArthur & Wilson's (1967) theory of island biogeography to the problem. However, many reserves, in the UK at least, are more likely to have their dimensions determined by constraints such as the willingness of landowners to sell their land and funds available to conservation organisations.

In the SLOSS debate, as in many academic studies of conservation, the main measure of success is the conservation of biodiversity. Usher (1986) notes that diversity heads the popularity poll of criteria to be used in conservation evaluation. In practice, however, it seems that single species (especially where these are rare, though possibly locally rather than globally rare) are the object of most conservation efforts, notably directed towards organisms with high public popularity, such as birds and mammals. The issues addressed in this thesis are, I hope, pertinent to actual conservation practice. This is not intended to dismiss more general conservation biology issues, but rather to show that modelling is a tool that can be of value in assisting practical conservation management decisions. In general this means dealing with situations where a single species is the focus of attention (though the techniques used here could be extended to multi-species situations). It is important to point out, however, that conservation measures focusing on a single species (or a few similar species) are not without problems. In Australia, for instance, conservation measures to preserve the kangaroo (combined with benefits from measures designed to benefit cattle and sheep) have allowed the numbers of red and grey kangaroos to grow to such a size that their wider environment is now threatened by habitat degradation as a result of the large number of kangaroos, and a cull is now being considered (Dayton 1991). Single species conservation measures are also not without problems in the Antarctic regions. The Antarctic fur seal, *Arctocephalus gazella*, was the first of Antarctica's resources to be exploited, and by 1822 was practically extinct on South Georgia (Bonner 1985). As further populations were discovered they too were exploited to the point of extinction. After the collapse of the sealing industry a small breeding population of fur seals was discovered on Bird Island to the north-west of South Georgia, which has shown extremely rapid growth since the 1930's (Bonner 1985). Since the Convention for the Conservation of Antarctic Seals came into force in 1978 the taking of fur seals has been completely banned (Sage 1985). However, as the population has recovered it has remained localised in this area and is only gradually beginning to recolonise sites where it was formerly numerous. Bonner (1985) notes that the unnaturally high concentrations of fur seals on Bird Island have resulted in much destruction of vegetation. Longton (1985) suggests that similar erosion of the few vegetated areas of Antarctica by penguins may be due to the lack of competition for krill caused by the reduction of whale stocks. Krill also makes up 90% of the fur seal diet (Bonner 1985). At some stage in the near future, conservation management may require that localised seal numbers be controlled in order to preserve the wider Antarctic environment, in particular the fragile vegetated areas.

Problems faced in model construction

In constructing a model to aid in species management there are likely to be several problems. In many cases the data available on the species population dynamics will be sparse and probably collected because of a researcher's interests rather than to provide the information required for model construction. While there may be a temptation to represent in a model all that is known or hypothesised about a species biology, a simple model for which parameters can be estimated is likely to be of more use in a management context than a complex model with many unknowns.

Most populations fluctuate, and to represent this in a simple model will often mean the incorporation of a random term. In general this is not meant to imply that the observed population size is the outcome of "pure chance". In some cases it is an admission of ignorance of the mechanisms producing the observed variation in population size. Shaffer (1987) points out that there is, in fact, little practical difference between a purely random event and an event that is unpredictable because it occurs as the result of processes that are not fully understood. However there may also be cases when the mechanisms producing the fluctuations are understood but the inputs nevertheless remain unpredictable (For example, variation in temperature causing variation in individual survival leading to fluctuations in the population size. The individual and population response to temperature may be well understood but the changes in temperature may remain unpredictable).

Shaffer (1981) suggests that the variability affecting population size can be divided into four categories: *demographic stochasticity*, arising from chance events in the survival and reproduction of a finite number of individuals; *environmental stochasticity*, temporal variation in both biotic and abiotic habitat parameters; *natural catastrophes*, occurring at random times; and *genetic stochasticity*, where changes in population size result from changes in gene frequencies.

An earlier classification of the variability affecting populations is that of Chesson (1978). What Shaffer terms demographic stochasticity, Chesson refers to as *within-individual* variability. Chesson points out that most models that consider such variation treat individuals equally: the distribution of birth and death probabilities for each individual is the same, variation in population size arising as a result of random 'sampling' from this distribution. Chesson terms *between-individual* variation the fact that, due to differences in phenotype, different individuals may, in fact, have different underlying probabilities of reproduction and survival. Chesson's (1978) other classes of variability are refined by Chesson (1985) who subdivides environmental variation into three classes: temporal environmental variation, spatial variation, and 'spatiotemporal' variation (where different spatial locations show independent fluctuations in environment through time, but spatial averages of the environment variables show no fluctuations through time and temporal averages do not vary in space).

Early models of the lifetime of populations focused on demographic (*within-individual*) stochasticity, modelled as birth and death processes (MacArthur & Wilson 1967, Richter-Dyn & Goel 1972). In such models, given a positive mean growth rate at small population sizes, persistence times tend to be very long once the population has exceeded a few tens of individuals (Goodman 1987a, Nisbet & Gurney 1982). In large populations the contribution of demographic stochasticity to fluctuations in size is insignificant compared to the contribution of environmental factors. However, Chesson (1978) suggests that demographic variability may be more important in populations which, in total, are large but which are subdivided with limited movement. Local subpopulations may be small enough in such cases that demographic stochasticity remains important.

Genetic factors affecting population persistence on ecological (as opposed to evolutionary) time scales, are only likely to be an issue when relatively small populations are considered. Shaffer (1987) reviews several studies and concludes that effective population sizes of 50 to 500 individuals are of the order necessary to provide security against the effects of inbreeding (the factor generally thought to have most effect on short term population survival). Such numbers should also prevent loss of genes through random genetic drift thus maintaining sufficient genetic diversity for continued adaptation. Shaffer suggests that a total number of individuals in the upper 100s to 1000s would provide such effective population sizes. Lande (1988) criticises the fact that these genetic criteria have been used as minimum necessary population sizes in some species management plans. Lande suggests that environmental stochasticity and local extinction and colonisation are likely to require much greater population sizes in order to ensure persistence of the species in question.

The models investigated in this thesis consider only temporal environmental variation and are thus most appropriate for larger populations where demographic and genetic effects on persistence are likely to be minimal. Catastrophic effects can often reasonably be considered as the extremes of environmental variation. For instance if weather conditions are included as a stochastic input to a population model then the tails of the distribution of 'weather states' may represent such extremes as violent storms or prolonged droughts. These natural catastrophes arise as extremes of typical inputs to the system. By contrast many man-made catastrophes, such as oil spills or toxic waste releases, can in no sense be considered a normal part of the biological system.

It is worth commenting that on a geological timescale, of course, all species eventually go extinct. Population management cannot hope to preserve species for ever. However, application of the methodology considered here may help population managers choose strategies which assist a species to persist in an environment which inevitably will be affected to some extent by the actions of the human race.

Criteria for judging the effect of management in stochastic models

Given that a population model has been constructed which incorporates environmental variation, the problem is how to assess the effects of different management strategies which may be incorporated into the model. An obvious candidate perhaps is the population growth rate. If a particular impact on the population could be shown to produce a negative population growth rate in the model then that particular strategy could be deemed to endanger the viability of the population and thus avoided. While suitable measures of long run population growth rate in a fluctuating environment do exist (Lewontin & Cohen 1969, Tuljapurkar & Orzack 1980) these would not be easy to apply in all circumstances. Consider, for instance, the case where the data on the population in question suggest that the population is not growing. This could be either because the population is truly "on the knife edge" between growth and decline, or because it is fluctuating around some mean value due to density dependent regulation. The detection of density dependence from population census data is notoriously difficult (Gaston & Lawton 1987, Murdoch & Walde 1989) and it will not always be possible to distinguish between the two possibilities. In addition we may sometimes want information on the impact of a fixed term effect on the population. This may produce a reduced, or negative, growth rate for the period but the question remains open as to whether this would greatly affect the population's longer term prospects of persistence.

Tuljapurkar & Orzack (1980) suggest that the triplet of long run growth rate, variance, and the probability distribution of crossing a boundary, is a valuable combination of measures for the description of population growth, distribution, and extinction. Here the focus is on the third, probably least studied (from a mathematical viewpoint), part of the triplet as a viability measure in population models.

Persistence time above a threshold as a population viability measure

The criterion used for assessing the stochastic population models considered here is based on the persistence time above some threshold population size. This gauge has been used before in the context of conservation. Shaffer (1983) used simulation models to assess the minimum population sizes required to provide probabilities of persistence for certain periods of time in the grizzly bear population of Yellowstone National Park and Dennis, Munholland & Scott (1991) have recently investigated persistence in various endangered bird populations under the assumption of a simple linear model. Ginzburg *et al.* (1982) recognised the value of using the time that the population persists above some threshold as a measure of the impact of an environmental change on a population, terming the reaching of the threshold "quasiextinction". Shaffer (1990) discusses 'population viability analysis' (PVA)

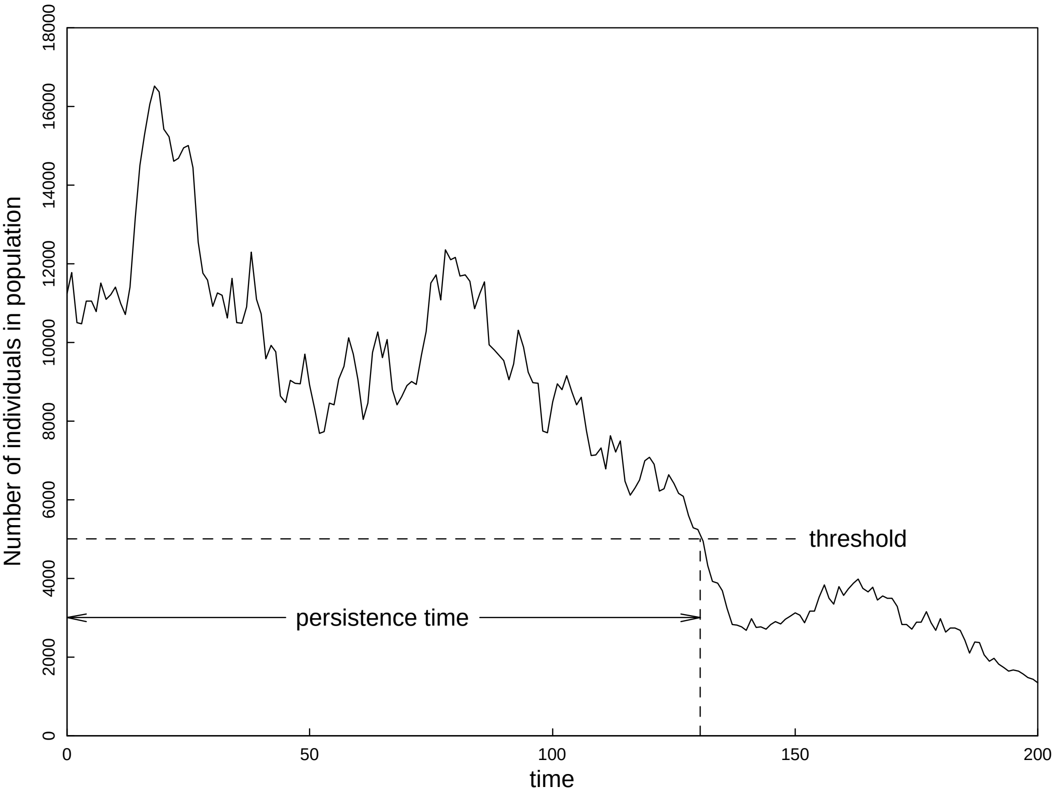


Figure 1.1. The persistence time is the first time that the population size reaches, or falls below, some threshold level given that it was above this level at the initial time considered.

which attempts to assess the likelihood of a population's extinction by some specified time under various scenarios of management, based on currently available data and theory (which both contain some uncertainty). Shaffer comments that, as yet, there are no widely accepted standards or methodology for the carrying out of such an analysis.

Given that the population is initially at a size greater than the threshold size of interest, then the persistence time is defined as the first time at which the population reaches, or falls below, the lower threshold size (Fig. 1.1). In the literature on stochastic processes this is known as the first passage time. As stochastic population models are being considered here, the population size at any time is a random variable. It follows that the first passage time is also a random variable; so it is the distribution of persistence times (and appropriate summary statistics of this distribution) that is of interest.

While this thesis focuses on persistence above a lower threshold, there may, of course, be cases where interest is in the time that a population remains *below* an upper threshold, or within certain bounds. For example, as noted earlier, there are instances where single-species conservation strategies have led to problems with the conserved population growing to such an extent that the wider ecosystem is degraded. Indeed, while much conservation effort focuses on relict populations, where the actions of mankind have led to reduced population size, there are also cases where human impact on the environment has led to the population growing well beyond its historical size. The time a population remains below an upper threshold, or within certain bounds, can also be addressed with the methodology considered in this thesis.

Lower threshold levels

Before considering the question of deciding at what level at which to set the lower threshold, it is necessary to address the issue of why the lower threshold is not simply zero. In other words, why consider persistence above a threshold rather than population extinction ?

In a management context threshold population sizes above zero are of obvious interest simply because conservation managers will become concerned not just when the managed population is extinct, but when it drops to low levels. In general the models constructed for management will be based on data from the usual range of population sizes. Fluctuations when the population is small may well be the result of very different processes to those that act to produce fluctuations in large populations. A lower threshold may therefore mark the limit of confidence in the current model.

As noted earlier, the models considered here represent only environmental stochasticity and population sizes is treated as a continuous variable. Nisbet & Gurney (1982) make the point that "..there is only one mechanism for extinction of a closed population - a single death in a population of exactly one individual". To consider true extinction, models should treat the population as discrete numbers of individuals, and consider factors such as demographic and genetic stochasticity which have greater impact as population size becomes small.

The setting of an appropriate lower threshold level is not necessarily easy. There are instances where lower thresholds can be chosen to have some particular biological significance. The concept of minimum viable population size (MVP) emerged in the early 1980s (Shaffer 1981, Gilpin & Soulé 1986) but while this resulted in useful attention being given to the processes threatening population persistence it quickly became clear that providing a general minimum population size rule for a range of species in different situations would not be possible (Soulé 1987). Sometimes, however, it may be possible to make recommendations for a particular population, based on good knowledge of the species biology. Boyd (1968) notes that 100,000 individuals is often considered to be the size below which north American goose populations should be protected from hunting as far as possible, though he does not explain how this figure was chosen. Shaffer's (1983) model suggested that a minimum population of 50 to 90 individuals was necessary to provide a 95% probability of persistence for 100 years for the Yellowstone grizzly bear population. Another possibility would be to use historical population sizes as a basis for assessing the appropriate lower threshold. In many cases however mankind's impact on the environment will make comparisons with past population sizes rather irrelevant.

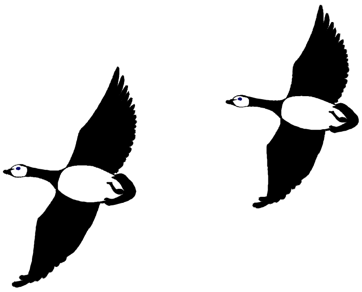
In practice, the lower threshold considered in any modelling exercise carried out to assess population management strategies is likely to be set rather arbitrarily. While it would be possible to define a threshold above which a population has a set probability of persisting for a certain amount of time in the manner suggested by Shaffer (1983) such statements are likely to have little practical value. More useful perhaps would be to consider several levels and consider the distribution of persistence times at each. In the general models considered in the first section the effect of different lower thresholds, relative to initial population size is examined. This insight is applied in the second section where persistence time is used as a measure of the viability of the Islay wintering barnacle goose population. Initial population size is, of course, fixed in this case and the choice of lower threshold makes quite a difference to the prediction of persistence time for the model with currently "measured" levels of environmental variability. For comparing the effects of different possible management strategies a single level is used chosen on the arbitrary basis that it represents a population size which would worry many conservationists should it occur.

I

Persistence in Simple Stochastic Population Models

This section grew from the desire to move away from the necessity for large simulation efforts to provide persistence time distributions. It does not, however, provide an analytical route for computing persistence time in any population model incorporating environmental variation. Instead it examines a number of simple, stochastic models where persistence time is analytically tractable to some extent, in order to provide a background on the methods that may prove useful, and the persistence time distributions that may arise. The models are chosen for their simplicity rather than their applicability to any particular managed population.

Chapter 2 lays the foundations for this work by surveying some of the results available in the literature for the first passage time distribution in well known stochastic processes. Using this background, chapter 3 examines persistence time in a general, linear population model and discusses some interesting ecological issues that arise. Chapter 4 makes a start at dealing with the problem of avoiding infinitely large populations in the linear model by examining the effect of a hard upper bound to population size. Despite the simplicity of the regulation method employed, an example, persistence time in sub-populations of the acorn woodpecker, demonstrates its applicability in a real population. Finally, chapter 5 investigates various methods of estimating persistence time in models which explicitly include density dependent regulation of population size.



Chapter 2

First passage time distributions of some simple stochastic processes

Chapter 1 noted that the problem of persistence time in stochastic population models corresponds to the problem of first passage time in the probability and stochastic processes literature. Compared with other areas of probability theory the first passage time problem is analytically difficult and therefore rather underdeveloped (Blake & Lindsey 1973), with results for all but the simplest processes largely unknown. Indeed it appears that many results have, in fact, been derived in response to another biological problem, namely the firing interval of neurones (Gerstein & Mandelbrot 1964, Capocelli & Ricciardi 1971, Favella *et al.* 1982). This chapter covers the basic ideas and terminology of stochastic processes necessary to consider the general mathematics of the first passage time. It also draws together various results relating to the first passage time in the Wiener and Ornstein-Uhlenbeck (OU) processes: this is done because the population models considered later in this section will be analysed in terms of these two well known stochastic processes. Both these processes are defined in continuous time and for a continuous state space. While these processes are relatively simple, results relating to the first passage time are spread throughout the literature of several disciplines. Here they are drawn together and expressed in a common terminology and notation. The results in this chapter have been checked by comparison with numerically estimated passage time distributions. In the one case (the Wiener process with an upper reflecting barrier) this numerical checking found errors in two published solutions.

By necessity, this chapter concentrates on the mathematics of the first passage time. However, gathering these results in one chapter provides the freedom to concentrate on ecological aspects of the persistence time in the following chapters.

Preliminaries, with examples from the random walk and Wiener process

Before proceeding to a general discussion of the first passage time it is useful to review some basic terminology; the idea of a diffusion equation (and the connection with stochastic differential/difference equations in which most population models are phrased [and numerically simulated]) is particularly important, as it is in such terms the first passage time is derived later. This section considers a simple stochastic process, its continuous time limit, and the connection with a diffusion equation.

Consider first one of the simplest stochastic processes: the simple, symmetrical random walk. The state variable, X_t (which describes the *state* of the process at time

t), takes integer values and changes at discrete times by either a positive or negative step of size one, with equal probability. (In all the population models considered later in this thesis, the state variable is some function of population size.) This is described by the stochastic difference equation

$$X_{t+1} = X_t + Z_{t+1} \qquad [2.1]$$

where t takes values 0, 1, 2, ... and the step Z_t has the probability distribution prob(Z_t = 1) = prob(Z_t = −1) = ½. Any particular sequence X_0, X_1, X_2, ... is known as a single *realisation* of the process. If the process takes the value zero at time zero (i.e. $X_0 = 0$) then at time $t = 1$ the state variable can take the value 1 (with probability = ½) or −1 (prob. = ½); at time $t = 2$, X takes either of the values −2 (prob. = ¼), 0 (prob. = ½), or 2 (prob. = ¼); and so on for t = 3, 4, ... Note that X_t can be either odd or even as t is odd or even. The probability that at some time, t, the state variable, X, takes some value, x, is given by the binomial distribution:

$$\text{prob}\left(X_t = x \middle| X_0 = 0\right) = \frac{t!}{\left[\tfrac{1}{2}(t+x)\right]!\left[\tfrac{1}{2}(t-x)\right]!}\left(\tfrac{1}{2}\right)^t \qquad [2.2]$$

This distribution has mean zero and standard deviation $\sqrt{t}$. For t large the distribution [2.2] converges to a normal distribution

$$p(x,t|0) = \left(\frac{1}{2\pi t}\right)^{\frac{1}{2}} \exp\left(\frac{-x^2}{2t}\right) \qquad [2.3]$$

where $p(x,t|0)$ is the *probability density* function. More generally, for a process at x_0 at time $t = 0$, $p(x,t|x_0)dx$ is the probability that X_t lies in the range [x, $x+dx$] at time t.

The continuous limit of the simple random walk [2.1] is obtained (Cox & Miller 1965, p.205–208) by considering small steps of magnitude Δx taking place at small time intervals of length Δt. Taking the more general (i.e. possibly asymmetric) random walk where p is the probability of a positive step and q the probability of a negative step then, to obtain a limiting process with mean μ and variance σ^2 in unit time, it is required that

$$\Delta x = \sigma\sqrt{\Delta t}, \qquad p = \frac{1}{2}\left(1 + \frac{\mu\sqrt{\Delta t}}{\sigma}\right), \qquad q = \frac{1}{2}\left(1 - \frac{\mu\sqrt{\Delta t}}{\sigma}\right) \qquad [2.4]$$

For the symmetric random walk considered above, μ is of course zero. The limiting process essentially involves summing a large number of independent random variables and appropriate scaling of the sum. This central limiting operation yields a normal distribution for the continuous variable $X(t)$ with mean μt and variance $\sigma^2 t$.

The important result here is that the change in position $\Delta X(t)$ in a small time interval Δt is of the order of magnitude $(\Delta t)^{½}$. For any two time instants k and t ($k > t > 0$) the increments $X(t) - X(0)$ and $X(k) - X(t)$ are independent, and the latter is normally distributed with mean $\mu(k - t)$ and variance $\sigma^2(k - t)$. The continuous process, $X(t)$, obtained as a limit of the symmetric random walk has $\mu = 0$ and is known as the Wiener process. Where the random walk is asymmetric the continuous analogue is known as the Wiener process *with drift*, μ.

The continuous time analogue of the stochastic difference equation [2.1] is a stochastic differential equation. In [2.1], Z_t is an independent, identically distributed random variable. Its continuous time counterpart, $Z(t)$, must be a purely random process, having the same distribution for all t and mutually independent values for distinct points in time. The difficulty with this process is that, due to its total lack of serial correlation, it is not a smooth function and so cannot be differentiated in the usual sense. The discussion of the limiting process above suggests that it is appropriate to write

$$X(t+\Delta t) = X(t) + Z(t)\sqrt{\Delta t} \qquad [2.5]$$

where $Z(t)$ is a Gaussian process with zero mean and unit variance. The change in the state of the process in a small time interval is then given by

$$\Delta X(t) = Z(t)\sqrt{\Delta t} \qquad [2.6]$$

A process with drift μ and variance σ^2 is obtained by writing

$$\Delta X(t) = \mu\Delta t + \sigma Z(t)\sqrt{\Delta t} \qquad [2.7]$$

This can be written as the differential equation for the Wiener process with drift

$$dX(t) = \mu dt + \sigma Z(t)\sqrt{dt} \qquad [2.8]$$

The derivative of the Wiener process without drift and with unit variance (which, as mentioned already, is not a derivative in the usual sense but what Turelli (1977) calls a generalised derivative) is known as Gaussian white noise. The Wiener increment, often denoted by dW, has a central role in the wider theory of stochastic differential equations, a general SDE being defined by

$$dX(t) = \alpha(x)dt + \beta(x)dW \qquad [2.9]$$

For a more complete outline of stochastic differential equations and the problems of white noise see Turelli (1977), Ricciardi (1977), Mortensen (1969) and Nisbet & Gurney (1982).

The derivation of the first passage time distribution considered next involves describing the model by a diffusion equation: a partial differential equation which describes the change in the probability density function $p(x,t|x_0)$ for continuous changes in state and time.

The diffusion equations for the Wiener process can be obtained by applying the limiting process considered earlier to the transition probabilities of the simple random walk (see Cox & Miller 1965, p.208–210). Consider small steps of size Δx occuring in small intervals Δt. For the general (i.e. possibly asymmetric) case where the probability of a positive step of size one in [2.1] is p, and a negative step has probability q, the transition probability can be written

$$p(x,t|x_0) = pp(x-\Delta x, t-\Delta t|x_0) + qp(x+\Delta x, t-\Delta t|x_0) \qquad [2.10]$$

Suppose $p(x,t|x_0)$ can be differentiated a suitable number of times and expanded in a Taylor series, i.e.:

$$p(x-\Delta x, t-\Delta t|x_0) = p(x,t|x_0) - \Delta t\frac{\partial p}{\partial t} + \Delta x\frac{\partial p}{\partial x} + \tfrac{1}{2}(\Delta x)^2\frac{\partial^2 p}{\partial x^2} + \ldots \qquad [2.11]$$

Expanding [2.10] in this way, using the relations [2.4], and letting $\Delta t \to 0$ yields the forward diffusion equation for the Wiener process

$$\frac{\partial}{\partial t}p(x|x_0,t) = \frac{1}{2}\sigma^2\frac{\partial^2}{\partial x^2}p(x|x_0,t) - \mu\frac{\partial}{\partial x}p(x|x_0,t) \qquad [2.12]$$

A diffusion equation takes the general form

$$\frac{\partial}{\partial t}p(x,t|x_0) = -\frac{\partial}{\partial x}\left[v(x)p(x,t|x_0)\right] + \frac{\partial^2}{\partial x^2}\left[w(x)p(x,t|x_0)\right] \qquad [2.13]$$

$v(x)$ and $w(x)$ are known as the infinitesimal mean and variance and can be thought of as describing the deterministic and stochastic parts of the process respectively (Turelli 1977). The initial value x_0 takes the form of a delta function: $p(x,0|x_0) = \delta(x-x_0)$.

The coefficients of the general stochastic differential equation [2.9] are related to the infinitesimal mean and variance of the corresponding diffusion equation. For the subset of stochastic differential equations where β is a constant and not a function of x, the relation is simply

$$v(x) = \alpha(x)$$
$$w = [\beta]^2 \qquad [2.14]$$

Note that the infintesimal variance, *w*, is also a constant in this case, rather than a function of *x* as in the general diffusion equation [2.13]. For cases where β is a function of the state variable, *x*, the relationship between the SDE and the diffusion equation is rather more complicated. This will be discussed further in chapter 5.

The first passage time

In chapter 1 the first passage time was defined heuristically in terms of the persistence time of a population over a threshold. Mathematically the first passage time to a level *a* for a process starting at x_0 can be defined by as the time *T* such that

$$X(0) = x_0 > a, \quad X(\tau) > a \;\; \forall \;\; 0 < \tau < T, \quad X(T) \le a$$

with probability density function $g(t|x_0, a)$.

In practice the first passage time is calculated by considering a changed stochastic process which has an "absorbing barrier" at the level to which we want to calculate the first passage time, such that all realisations reaching this level remain there. Thus, for the first passage time to some low level $x = a$ (where $a < x_0$) the process is constrained to the interval $[a, \infty]$. This requires a boundary condition on the diffusion equation [2.13], namely

$$p(a, t|x_0) = 0 \qquad [2.15]$$

Now let $P(t|x_0, a) = \text{prob}\{T \ge t\}$ be the probability that absorption at the barrier *a* has not occurred by time *t* i.e.

$$P(t|x_0, a) = \int_{a^+}^{\infty} p(x, t|x_0, a)dx = \text{prob}\left\{X(\tau) > a \;\forall\; 0 < \tau < t, X(t) \le a \middle| X(0) = x_0\right\} \qquad [2.16]$$

where a^+ is infinitesimally above the absorbing barrier *a*, thus avoiding integrating over the δ–function at *a* which is created by the boundary condition [2.15]. $P(t|x_0, a)$ is either constant or monotonically decreasing. The probability density function of the first passage time, $g(t|x_0, a)$, is the negative of the rate of decrease of $P(t|x_0, a)$, the probability that absorption has not occurred by time *t*. Thus

$$g(t|x_0, a) = -\frac{d}{dt}P(t|x_0, a) \qquad [2.17]$$

Substituting from [2.16], changing the order of integration, then substituting from [2.13] (with *w* constant) gives

$$g(t|x_0,a) = -\int_{a^+}^{\infty} \frac{\partial}{\partial t} p(x,t|x_0,a)dx = -\int_{a^+}^{\infty} \left(\frac{1}{2} w \frac{\partial^2}{\partial x^2} p(x,t|x_0,a) - \frac{\partial}{\partial x}\left[v(x) p(x,t|x_0,a) \right] \right) dx$$

$$= -\left[\frac{1}{2} w \frac{\partial}{\partial x} p(x,t|x_0,a) - v(x) p(x,t|x_0,a) \right]_a^{\infty} = \frac{1}{2} w \frac{\partial}{\partial x} p(x,t|x_0,a) \bigg|_a \qquad [2.18]$$

as $p(a,t|x_0,a) = 0$ and +∞ is a natural boundary.

This is a general method for linking the probability density function for *x*, $p(x,t|x_0,a)$, to the probability density function for the first passage time *T*, $g(t|x_0,a)$, for a continuous state space, continuous time stochastic process confined by a single absorbing barrier.

An important function of the first passage time is the probability of ultimate absorption at the barrier, *a*, which is simply the area under the curve defined by the first passage time probability density function

$$G(\infty|x_0) = \int_0^{\infty} g(t|x_0,a) dt \qquad [2.19]$$

If $G(\infty)$ does not equal one then the first passage time distribution is an *improper* probability distribution.

First passage times of some simple stochastic processes

The Wiener process

The Wiener process, introduced above as the limit of the simple random walk, is probably the best known continuous state space, continuous time stochastic process. Here both the standard symmetrical Wiener process and the Wiener process with drift are considered. These arise as approximations to multiplicative population models with density independent vital rates.

The stochastic differential equation for the Wiener process was given at [2.8]. Using the relations [2.14] the forward diffusion equation is given by

$$\frac{\partial}{\partial t} p(x|x_0,t) = \frac{1}{2}\sigma^2 \frac{\partial^2}{\partial x^2} p(x|x_0,t) - \mu \frac{\partial}{\partial x} p(x|x_0,t) \qquad [2.20]$$

where μ is the drift term and σ^2 is the infinitesimal variance. This, of course, coincides with the diffusion equation [2.12] found by applying a limiting process to the transition probabilities of the simple random walk [2.1]. The no drift case is obtained by setting μ equal to zero. The solution of this diffusion equation is well known (e.g. Cox and Miller, 1965)

$$p(x,t|x_o) = \frac{1}{\sigma\sqrt{2\pi t}} \exp\left(\frac{\left(x - x_0 - \mu t\right)^2}{2\sigma^2 t} \right) \qquad [2.21]$$

Thus, in accordance with the previous limiting operations, the probability density of the Wiener process is seen to be normally distributed with mean and variance of the increment $X(t) - X(0)$ given by μt and $\sigma^2 t$ respectively.

The first passage time distribution

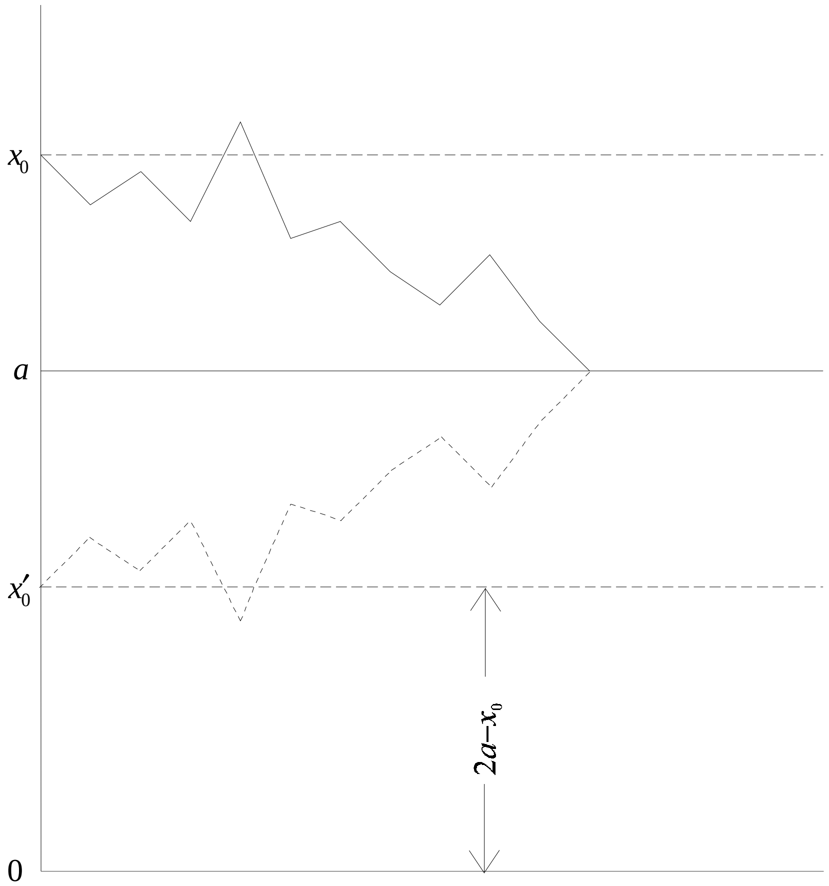


Figure 2.1 The method of images: a sample path and its reflection in the absorbing barrier. The reflection principle states that the number of paths from x_0 to x_t which touch or cross the level a is equal to the number of all paths from x_0' to x_t (Feller 1968).

As in the general case above the first passage time of the Wiener process to a level a ($a < x_0$) is obtained by considering an absorbing barrier at $x = a$. This necessitates the imposition of the boundary condition

$$p(a,t|x_0) = 0 \tag{2.22}$$

on the diffusion equation [2.20]. To solve for $p(x,t|x_0,a)$ in this changed process a number of methods could be used. For this particular boundary condition the *method of images* is commonly used (e.g. Cox and Miller 1965). This requires considering an "image source", x_0', at the reflection of x_0 in the barrier a: $x_0' = a-(x_0-a) = 2a-x_0$ (see Fig. 2.1).

As equation [2.20] is linear and homogeneous the superposition principle holds. A possible solution is therefore

$$p(x,t|x_0,a) = p(x,t|x_0) - Ap(x,t|(2a-x_0))$$

where A is chosen to ensure that the boundary condition [2.22] holds.

Putting $A = \exp\left(\frac{2\mu(a-x_0)}{\sigma^2}\right)$ and substituting from [2.21] gives

$$\begin{aligned} p(x,t|x_0,a) = \frac{1}{\sigma\sqrt{2\pi t}} & \left[\exp\left(\frac{-(x-x_0-\mu t)^2}{2\sigma^2 t}\right)\right. \\ & \left. - \exp\left(\frac{2\mu(a-x_0)}{\sigma^2} - \frac{(x-2a+x_0-\mu t)^2}{2\sigma^2 t}\right)\right] \end{aligned} \tag{2.23}$$

which satisfies the diffusion equation [2.20] and boundary condition [2.22]. The probability density function [2.23] for the Wiener process with a lower absorbing barrier differs from the probability density function for the unrestricted process [2.21] by the presence of a term which reduces the probability remaining in the interval $[a^+, \infty]$ as t increases. This is due to the fact that realisations reaching the absorbing boundary a stay there. The first passage time distribution is obtained the by using the result [2.18] above

$$\begin{aligned}
g(t|x_0,a) &= \frac{1}{2}\sigma^2 \frac{\partial}{\partial x} p(x,t|x_0,a)\Big|_a \\
&= \frac{1}{2}\sigma^2 \frac{1}{\sigma\sqrt{2\pi t}} \exp\left(-\frac{(a-x_0-\mu t)^2}{2\sigma^2 t}\right)\left[\frac{\mu(a-x_0-\mu t)}{\sigma^2 t} + \frac{(a-x_0-\mu t)^2}{2\sigma^2 t^2} - \frac{1}{2t}\right] \qquad [2.24] \\
&= \frac{x_0-a}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{(a-x_0-\mu t)^2}{2\sigma^2 t}\right)
\end{aligned}$$

In the statistical literature this distribution is known as the Inverse Gaussian distribution and a number of features can be gleaned from this literature (Johnson & Kotz 1970, Lande & Orzack 1988).

The probability of ultimate absorption

Substituting [2.24] in the expression for the probability of ultimate absorption at the lower boundary, *a*, [2.19] yields

$$G(\infty|x_0) = \begin{cases} 1 & (\mu \le 0) \\ \exp\left(-\frac{2\mu}{\sigma^2}(x_0-a)\right) & (\mu > 0) \end{cases} \qquad [2.25]$$

Thus for cases with drift away from the absorbing barrier ($\mu > 0$) there is a finite chance that the process will never reach the absorbing barrier. In such cases the probability density function for the first passage time is an improper distribution as the area under the curve does not integrate to one. A proper probability distribution can be obtained by dividing the original distribution of passage times by the probability of ultimate absorption to give the distribution of passage times *conditional* on ultimate absorption:

$$g^*(t|x_0,a) = \frac{g(t|x_0,a)}{G(\infty|x_0)}$$

So, for $\mu > 0$

$$\begin{aligned}
g^*(t|x_0,a) &= \frac{\frac{x_0-a}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{(a-x_0-\mu t)^2}{2\sigma^2 t}\right)}{\exp\left(-\frac{2\mu}{\sigma^2}(x_0-a)\right)} \qquad [2.26] \\
&= \frac{(x_0-a)}{\sigma\sqrt{2\pi t^3}} \exp\left(\frac{-(a-x_0+\mu t)^2}{2\sigma^2 t}\right)
\end{aligned}$$

Thus, for any μ, the conditional probability distribution is

$$g^*(t|x_0,a) = \frac{x_0 - a}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{(a - x_0 + |\mu| t)^2}{2\sigma^2 t} \right) \quad [2.27]$$

Moments of the first passage time distribution

The moments for the conditional distribution are (Capocelli & Ricciardi 1974)

$$\text{mean} = \frac{(x_0 - a)}{|\mu|} \quad [2.28]$$

$$\text{variance} = \frac{\sigma^2 (x_0 - a)}{|\mu|^3} \quad [2.29]$$

Thus for the no drift case, $\mu = 0$, the mean and variance of the first passage time are infinite.

The shape of the first passage time distribution [2.24] is determined by a parameter ϕ (Johnson & Kotz 1970), where

$$\phi = \frac{\mu(x_0 - a)}{\sigma^2} \quad [2.30]$$

As ϕ increases the first passage time probability density function becomes more symmetrical, with the mode approaching the mean as ϕ tends to infinity.

For many cases of interest in a population context (examples will be found in chapters 3 and 7), the first passage time distribution tends to be skewed, with a long tail to longer times. The mode of the distribution is also therefore of interest. For the unconditional distribution the mode is (Johnson & Kotz 1970, Capocelli & Ricciardi 1974)

$$\text{mode} = \begin{cases} \dfrac{(x_0 - a)^2}{3\sigma^2} & (\mu = 0) \\ \dfrac{(x_0 - a)}{|\mu|}\left(1 + \dfrac{9\sigma^4}{4\mu^2 (x_0 - a)^2}\right)^{\frac{1}{2}} - \dfrac{3\sigma^2}{2\mu^2} & (\mu \neq 0) \end{cases} \quad [2.31]$$

A special case: the Wiener process with an upper reflecting barrier

In chapter 4 a population model with density independent vital rates and a crude form of regulation, a hard upper bound to population size, is considered. Persistence time in this model is approximated by considering another change to the Wiener process:

the imposition of a reflecting barrier at the level of the upper limit. Like the absorbing boundary the reflecting boundary prevents the process from passing that level. However, while the absorbing boundary traps the process at the boundary, a reflecting boundary allows the process to leave the boundary and return into the interval over which the process is defined. Consider a Wiener process confined to an interval [a, b] (with $a < x_0 < b$) with a absorbing and b reflecting. The behaviour at the reflecting barrier is represented as a further boundary condition on the diffusion equation [2.20] (Cox & Miller 1965, p. 223-225)

$$\left[\frac{1}{2}\sigma^2\frac{\partial p\left(x,t\middle|x_0,a,b\right)}{\partial x}-\mu p\left(x,t\middle|x_0,a,b\right)\right]_{x=b}=0 \qquad [2.32]$$

This boundary condition is derived by considering the Wiener process with a single reflecting barrier at b ($b > x_0$). Realisations are therefore limited to the region [$-\infty$, b]. Thus

$$\int_{-\infty}^{b} p\left(x,t\middle|x_0\right)dx=1 \qquad [2.33]$$

Unlike the absorbing boundary considered above which, by trapping realisations at the boundary caused a decrease in the probability density in the interval [a^+, ∞] as time increased, there is no "loss" of probability associated with a reflecting barrier. Consequently

$$\frac{\partial}{\partial t}\int_{-\infty}^{b} p\left(x,t\middle|x_0\right)dx=\int_{-\infty}^{b}\frac{\partial}{\partial t}p\left(x,t\middle|x_0\right)dx=0 \qquad [2.34]$$

Substituting [2.20] in [2.34] yields the boundary condition [2.32] above.

Diffusion equations with more complex boundary conditions, such as this, are generally solved using eigenvalue methods, rather than the method of images. However, both "solutions" of the diffusion equation for the Wiener process with one absorbing and one reflecting barrier found in the literature (Goel & Richter-Dyn 1974, Sweet & Hardin 1970) are, in fact, incorrect. Roy Veitch (pers. comm., Dept. Statistics & Modelling Science, University of Strathclyde) has produced a corrected version of Sweet & Hardin's analysis. [Schwarz (1992), apparently unaware of Sweet & Hardin's work, has also recently tackled the problem of the Wiener process with an absorbing and reflecting barrier].

The required probability density function is (Veitch, pers. comm.):

$$\begin{aligned} p\left(x,t \middle| x_0, a, b\right) &= \exp\left(-\frac{\mu^2 t}{2\sigma^2} - \frac{\mu}{\sigma^2}(x_0 - x)\right)\frac{2}{b-a} \\ &\quad \times \sum_{n=1}^{\infty}\left[\exp\left(-\frac{\lambda_n^2 \sigma^2 t}{2}\right)\frac{\lambda_n^2}{\lambda_n^2 + \left(\dfrac{\mu}{\sigma^2}\right)^2 - \dfrac{\mu}{(b-a)\sigma^2}} \right. \\ &\quad \left. \times Y_n(b-x)Y_n(b-x_0)\right] + \exp\left(-\frac{\mu}{\sigma^2}(x_0 - x)\right)h \end{aligned} \qquad [2.35]$$

where

$$Y_n(x) = \cos(\lambda_n x) - \frac{\mu}{\sigma^2 \lambda_n}\sin(\lambda_n x) \qquad [2.36]$$

the "eigenvalues" λ_n satisfy

$$\tan(\lambda_n(b-a)) = \frac{\lambda_n \sigma^2}{\mu} \qquad [2.37]$$

such that $0 < \lambda_1 < \lambda_2 < \ldots$, and

$$h = \begin{cases} 0 & \text{if } \dfrac{\mu(b-a)}{\sigma^2} < 1 \\[2ex] \exp\left(-\dfrac{\mu^2 t}{2\sigma^2}\right)\dfrac{3}{(b-a)^3}(a-x)(a-x_0) & \text{if } \dfrac{\mu(b-a)}{\sigma^2} = 1 \\[2ex] \exp\left(-\dfrac{\sigma^2 t}{2}\left[\left(\dfrac{\mu}{\sigma^2}\right)^2 - q^2\right]\right) & \\ \quad \times \dfrac{2q^2}{(b-a)\left(q^2 - \left(\mu/\sigma^2\right)^2\right) + \mu/\sigma^2} & \text{if } \dfrac{\mu(b-a)}{\sigma^2} > 1 \\ \quad \times V(b-x)V(b-x_0) & \end{cases} \qquad [2.38]$$

where

$$V(x) = \cosh(qx) - \frac{\mu}{q\sigma^2}\sinh(qx) \tag{2.39}$$

and q is the positive solution of

$$\tanh\left(q(b-a)\right) = \frac{q\sigma^2}{\mu} \tag{2.40}$$

When computing the probability density function some care must be taken in finding the eigenvalues, a fact which is not immediately obvious from the notation used here (which follows that of Sweet & Hardin) (Roy Veitch pers. comm.). This becomes apparent if the eigenvalue equation is written in the form $\tan(z) = mz$, where $m = \frac{\sigma^2}{\mu(b-a)}$. Then the eigenvalues are obtained from the values of z at which the line $y = mz$ intersects the curve $y = \tan(z)$. The intersections z_1, z_2,.. give $\lambda_1(b - a)$, $\lambda_2(b - a)$,... There are four cases of interest, illustrated in Fig. 2.2, which demonstrates that the case $\frac{\mu}{\sigma^2}(b-a) < 1$ in [2.38] actually covers two situations:

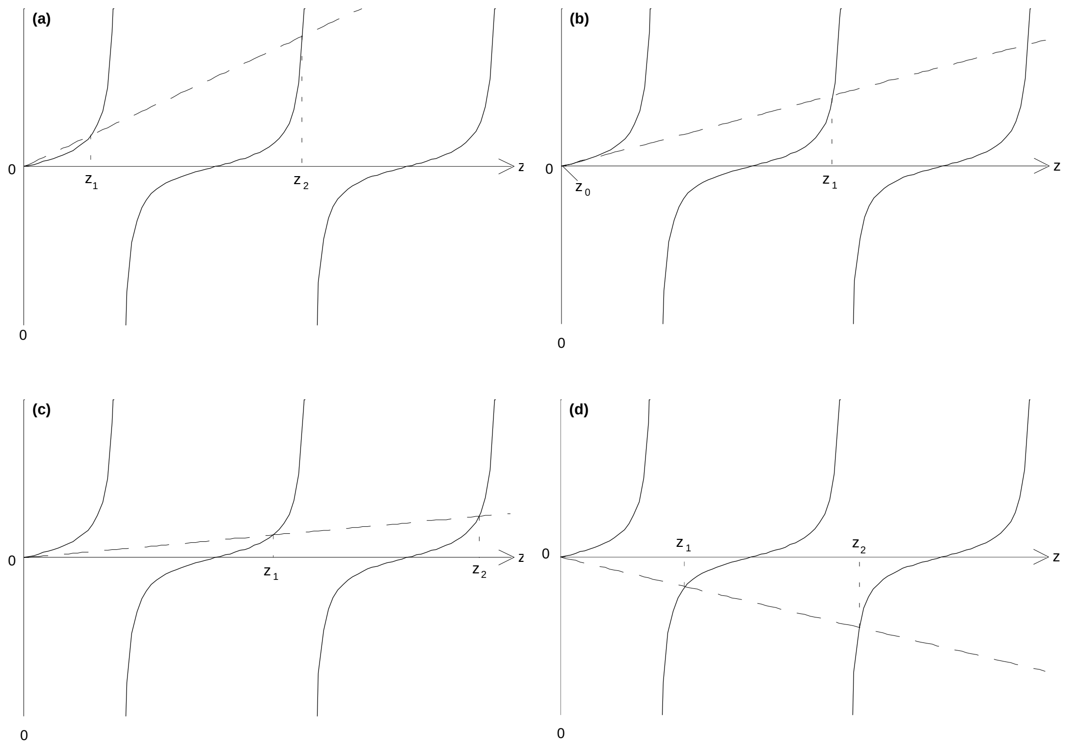


Figure 2.2 Intersection of the line $y = mz$ with the curve $y = \tan(z)$, for different values of m. (a) $m > 1$, (b) $m = 1$, (c) $0 < m < 1$, (d) $m < 0$.

$m > 1$ $\left(0<\frac{\mu}{\sigma^2}(b-a)<1\right)$, and $m < 0$ $\left(\frac{\mu}{\sigma^2}(b-a)<0\right)$. When $m > 1$ there is an "extra" eigenvalue due to the intersection of the line $y = mz$ with the tan curve which passes through the origin.

The procedure for obtaining the first passage time distribution is similar to that used for the general single barrier case above [2.18]

$$
\begin{aligned}
g(t|x_0,a) &= -\frac{d}{dt}\int_a^b p(x,t|x_0,a,b) = -\int_a^b \frac{\partial}{\partial t} p(x,t|x_0,a,b)dx \\
&= -\int_a^b \left(\frac{1}{2}\sigma^2 \frac{\partial^2}{\partial x^2} p(x,t|x_0,a,b) - \frac{\partial}{\partial x}\left[\mu p(x,t|x_0,a,b)\right]\right)dx \\
&= -\left[\frac{1}{2}\sigma^2 \frac{\partial}{\partial x} p(x,t|x_0,a,b) - \mu p(x,t|x_0,a,b)\right]_a^b = \frac{1}{2}\sigma^2 \frac{\partial}{\partial x} p(x,t|x_0,a,b)\Big|_a
\end{aligned}
$$

as $p(a,t|x_0,a,b) = 0$ and $\left[\frac{1}{2}\sigma^2 \frac{\partial}{\partial x} p(x,t|x_0,a,b) - \mu p(x,t|x_0,a,b)\right]_{x=b} = 0$

This leads to the probability density function for the first passage time distribution

$$
\begin{aligned}
g(t|x_0,a,b) &= \exp\left(-\frac{\mu^2 t}{2\sigma^2} - \frac{\mu}{\sigma^2}(x_0-a)\right)\frac{\sigma^2}{b-a} \\
&\quad \times \sum_{n=1}^{\infty}\left[\exp\left(-\frac{\lambda_n^2\sigma^2 t}{2}\right)\frac{\lambda_n \sin(\lambda_n(b-a))}{1-\frac{\mu}{\lambda_n^2(b-a)\sigma^2}\sin^2(\lambda_n(b-a))} Y_n(b-x_0)\right] \\
&\quad + \exp\left(-\frac{\mu^2 t}{2\sigma^2} - \frac{\mu}{\sigma^2}(x_0-a)\right)\frac{\sigma^2}{2(b-a)}k \qquad [2.41]
\end{aligned}
$$

where

$$k = \begin{cases} 0 & \text{if } \dfrac{\mu(b-a)}{\sigma^2} < 1 \\ \dfrac{3(x_0 - a)}{(b-a)^2} & \text{if } \dfrac{\mu(b-a)}{\sigma^2} = 1 \\ \exp\left(\dfrac{q^2\sigma^2 t}{2}\right) \times \dfrac{2q\sinh(q(b-a))}{-1+\sinh^2(q(b-a))\,\mu\,/\left(\sigma^2(b-a)q^2\right)} V(b-x_0) & \text{if } \dfrac{\mu(b-a)}{\sigma^2} > 1 \end{cases} \qquad [2.42]$$

Note that this result cannot be used for cases where the drift velocity is zero ($\mu = 0$). However, Goodman (1987a) noted that, in this no drift case, a Wiener process on the interval [*a*, *b*] where *a* is absorbing and *b* reflecting, is equivalent to a process on the interval [*a*, (2*b* – *a*)] with both end states absorbing (Fig. 2.3).

The Wiener process with two absorbing barriers

Consider the case where the Wiener process is constrained by absorbing barriers to the interval [*a*,*b*] (where $a < x_0 < b$). This satisfies the diffusion equation [2.20] with the additional boundary condition $p(b,t|x_0) = 0$. To solve this requires a rather more complex image system than the single barrier case above (as we must allow for images of images etc.). In fact a doubly infinite system of images is needed. Following Cox and Miller (1965, p.222) this is denoted by sources at the points x'_n (n = ±1, ±2,...) with strength $\exp(\mu x'_n / \sigma^2)$ and x''_n with strength $-\exp(\mu x''_n / \sigma^2)$ where $x'_n = 2n(b - 2x_0 + a)$ and $x''_n = 2n(b - x_0) - x'_n$. The superposition of the solution for each source, weighted by the corresponding strength, gives the required probability density function

$$p(x,t|x_0,a,b) = \frac{1}{\sigma\sqrt{2\pi t}} \sum_{n=-\infty}^{\infty} \left[\exp\left(\frac{\mu x'_n}{\sigma^2} - \frac{(x - x'_n - \mu t)^2}{2\sigma^2 t} \right) - \exp\left(\frac{\mu x''_n}{\sigma^2} - \frac{(x - x''_n - ut)^2}{2\sigma^2 t} \right) \right] \qquad [2.43]$$

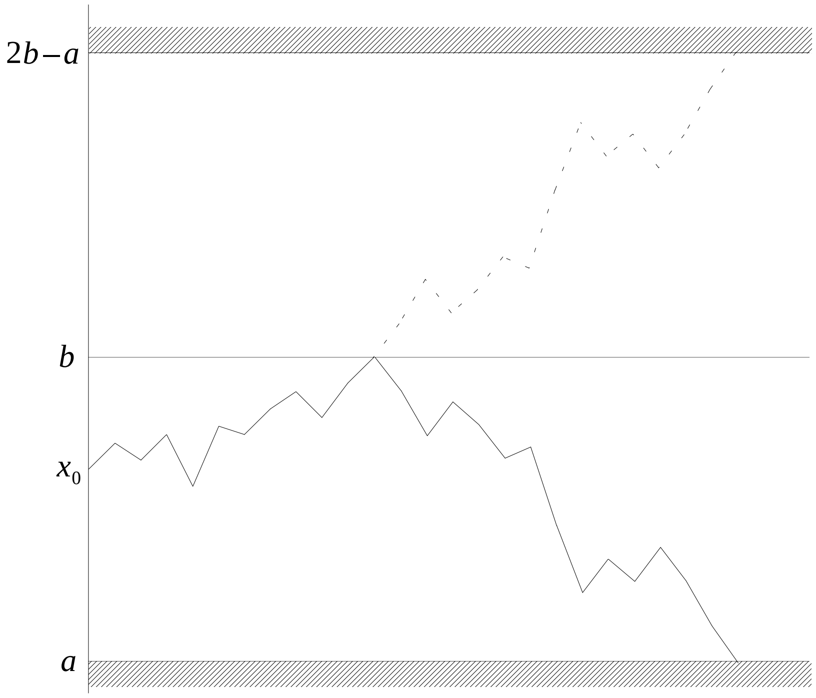


Figure 2.3 Illustration of Goodman's method for the first passage time with an absorbing barrier at *a* and a reflecting barrier at *b* for the Wiener process with no drift. The first passage time distribution for trajectories starting from x_0 with absorption at *a* and *b* reflecting is equivalent to the distribution with *a* and (2*b* – *a*) both absorbing.

While the first passage time probability density function could be found by extending the single barrier methods used previously, this is not, in fact, necessary here as the only result required in this thesis is for the no drift case ($\mu = 0$) which is used to provide the first passage time for the case with a lower absorbing and upper reflecting barrier using Goodman's method. This is given by Darling and Siegert (1953) (who also assume $\sigma^2 = 1$)

$$g\left(t \middle| x_0, a, b\right) = \frac{\pi}{\left((b-a)/2\right)^2} \sum_{n=0}^{\infty} \left[(-1)^n \left(n+\tfrac{1}{2}\right) \times \cos\left(\left(n+\tfrac{1}{2}\right) \frac{\pi\left(x_0 - \left((b+a)/2\right)\right)}{(b-a)/2} \right) \exp\left(\frac{-\left(n+\tfrac{1}{2}\right)^2 \pi^2 t}{2\left((b-a)/2\right)^2} \right) \right] \qquad [2.44]$$

Darling and Siegert's result can be generalised for cases with non-unit variance by recognising that a Wiener process on the interval [*a*, *b*] with $a < x_0 < b$ with arbitrary variance is equivalent to a process on $\left[\frac{a}{\sigma}, \frac{b}{\sigma}\right]$ with $\frac{a}{\sigma} < \frac{x_0}{\sigma} < \frac{b}{\sigma}$ and $\sigma^2 = 1$.

The probability of ultimate absorbtion for the Wiener process with an upper reflecting barrier

For the Wiener process on the interval [*a*, ∞] with positive drift there was a finite chance that absorbtion at *a* would never take place (see [2.25]) as a realisation could continue growing to infinity. For a finite reflecting barrier, *b*, such escape from absorption at *a* is not possible. Whilst it is possible to obtain an expression for the probability of ultimate absorbtion by direct integration of [2.41], consider instead the following argument (Veich, pers. comm.), where *G*(*T*) is the probability of absorbtion by time *T*:

$$\begin{aligned} G(T) &= \int_0^T g(t)dt = \int_0^T -\frac{d}{dt}\int_a^b p(x,t|a,b)dx\,dt \\ &= -\int_a^b p(x,t|a,b)dx\Big|_{t=0}^{t=T} \\ &= -\int_a^b p(x,T|a,b)dx + \int_a^b p(x,0|a,b)dx \\ &= -\int_a^b p(x,T|a,b)dx + 1 \end{aligned}$$

Thus

$$G(\infty) = 1 - \int_a^b p(x,\infty|a,b)dx \qquad [2.45]$$

Integration of [2.35] over the range [*a*, *b*] will produce a sum of terms each of which has a factor e^{-t}. For $t = \infty$ all these terms will be zero, and the integral in [2.45] will be zero. Thus *G*(∞) = 1 for all finite reflecting barriers.

The expected first passage time for the Wiener process with an upper reflecting barrier

Cox and Miller (1965, p.234) give the expected first passage time for the Wiener process with an absorbing and a reflecting barrier

$$E\left(T\middle|x_0,a,b\right)=\begin{cases}\dfrac{\sigma^2}{2\mu^2}\exp\left(\dfrac{2\mu(b-a)}{\sigma^2}\right)\left[1-\exp\left(-\dfrac{2\mu(x_0-a)}{\sigma^2}\right)\right.\\ \qquad\left.-\dfrac{2\mu(x_0-a)}{\sigma^2}\exp\left(-\dfrac{2\mu(b-a)}{\sigma^2}\right)\right] & \mu\neq 0\\ \\ \dfrac{(x_0-a)(2b-a-x_0)}{\sigma^2} & \mu=0\end{cases}\qquad [2.46]$$

The Ornstein Uhlenbeck process

The Ornstein Uhlenbeck (OU) process is another well known stochastic process. It was introduced by Uhlenbeck & Ornstein (1930) as an alternative to the Wiener process as a model for Brownian motion. In the context of the population models considered in this thesis it will be used to provide the persistence time in density dependent models (chapter 5), where it arises both as a transformation of a logistic model with random carrying capacity and as a local linearisation about the equilibrium for a large class of density dependent models. The OU process can be represented by the stochastic differential equation

$$dX(t)=-\mu x dt+\sigma Z(t)\sqrt{dt} \qquad [2.47]$$

(conditional on $X(t) = x$) and has diffusion equation

$$\frac{\partial}{\partial t}p\left(x\middle|x_0,t\right)=\frac{1}{2}\sigma^2\frac{\partial^2}{\partial x^2}p\left(x\middle|x_0,t\right)+\mu\frac{\partial}{\partial x}xp\left(x\middle|x_0,t\right) \qquad [2.48]$$

The probability density function for the OU process is normal with mean and variance given by

$$E(X(t))=x_0\exp(-\mu t),\qquad Var(X(t))=\frac{\sigma^2}{2\mu}(1-\exp(-2\mu t)) \qquad [2.49]$$

As $t\rightarrow\infty$ a normal distribution with mean zero and variance $\sigma^2/2\mu$ results (Cox & Miller 1965). For the population models considered later, the OU state variable, $X(t)$, (which can be positive or negative) represents the deviation of population size (or some function of population size) from the mean population size, which is represented by the asymptotic zero mean of the OU process.

The first passage time

Later in this section the first passage time for the OU process to a lower absorbing barrier, a, where $a < x_0$ and $a < 0$ will be of interest. The full first passage time distribution has only been obtained for the case where $a = 0$ (Darling & Siegert 1953, Blake & Lindsey 1973). This is relatively uninteresting as zero is the asymptotic mean of the OU process and is equivalent to mean population size in the models of considered in chapter 5. However exact results are available for the moments of the general first passage time problem (Sato 1978, Cerbone, Ricciardi & Sacerdote 1981, Ricciardi & Sato 1988), together with various approximations both to the moments (Thomas 1975, Sato 1978, Ricciardi & Sato 1988) and the distribution (Ricciardi & Sato 1988).

The expected first passage time

Exact expressions for the expected first passage time for the OU process with a single absorbing barrier are given by several authors (Sato 1977; Cerbone, Ricciardi & Sacerdote 1981; Nobile, Ricciardi & Sacerdote 1985). The form given below is that of Cerbone, Ricciardi & Sacerdote (1981) as their power series are computationally easier than some of the other forms in the literature. Cerbone, Ricciardi & Sacerdote obtained their expressions for the case of an upper absorbing barrier, $x_0 < a$. However, due to the symmetry of the OU process $-x_0$ can be substituted for x_0 and $-a$ for a (Nobile, Ricciardi & Sacerdote 1985), giving

$$\begin{aligned} E\left(T \middle| x_0, a\right) = \frac{1}{\mu}\Bigg[& \frac{1}{2}\left(\psi\left[-a\left(\frac{\sigma^2}{2\mu}\right)^{-\frac{1}{2}}\right] - \psi\left[-x_0\left(\frac{\sigma^2}{2\mu}\right)^{-\frac{1}{2}}\right]\right) \\ & + \left(\frac{\pi}{2}\right)^{\frac{1}{2}}\left(\chi\left[-x_0\left(\frac{\sigma^2}{2\mu}\right)^{-\frac{1}{2}}\right] - \chi\left[-a\left(\frac{\sigma^2}{2\mu}\right)^{-\frac{1}{2}}\right]\right)\Bigg] \end{aligned} \qquad [2.50]$$

where

$$\begin{aligned} \psi[z] &= \sum_{n=1}^{\infty} \frac{z^{2n}}{n(2n-1)!!} \\ \chi[z] &= -z\sum_{n=0}^{\infty} \frac{z^{2n}}{2^n n!(2n+1)} \end{aligned} \qquad [2.51]$$

The double factorial, $x!!$, is equal to $x.(x-2).(x-4)....$ where the last factor is either 1, if x is odd, or 2, if x is even.

Cerbone, Ricciardi & Sacerdote also give exact expressions for the variance and skewness of the OU process first passage time. More recent work by Nobile, Ricciardi & Sacerdote (1985) and Ricciardi & Sato (1988) gives insight into the distribution of passage times. For a fixed initial state, x_0, (where $-x_0 < -a$), as $|a|$ increases, an exponential first passage time probability density function arises with mean equal to the mean first passage time from zero to the boundary:

$$g\left(t|x_0,a\right)=\frac{1}{E\left(T|0,a\right)}\exp\left(-\frac{t}{E\left(T|0,a\right)}\right)+o\left[\frac{1}{E\left(T|0,a\right)}\exp\left(-\frac{t}{E\left(T|0,a\right)}\right)\right] \quad [2.52]$$

where $E\left(T|0,a\right)$ is given by [2.50] above. A similar asymptotic result arises for large times.

Ricciardi & Sato suggest approximating the mean first passage time, for $|a|$ large, by $1/k(a)$ where

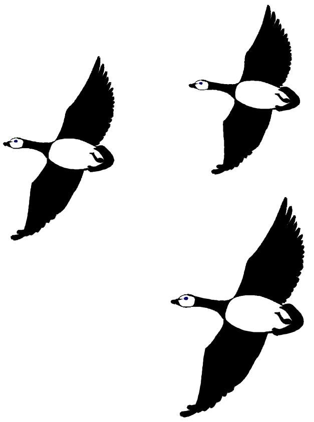
$$k(a)=\frac{a}{\sqrt{2\pi}}\exp\left(-\frac{a^2}{2}\right) \quad [2.53]$$

For small t, $g\left(t|x_0,a\right)$ is of order $\exp\left(-\left(x_0-a\right)^2/2t\right)$ (Ricciardi & Sato 1988).

Comments on results from the literature

This review has brought together a range of first passage time results which can be used to investigate persistence time in simple stochastic population models. Such results tend to be widely scattered in the literature and, as the problem of obtaining the probability density function for the Wiener process with an upper reflecting barrier has shown, published results may well be inaccurate. While the first passage time distribution for the simple Wiener process is easily obtained, the increase in complexity when a reflecting barrier is added, and the lack of exact results for the OU process first passage time distribution, tend to suggest that closed form results for the persistence time distributions of more complex stochastic population models than those considered in the next few chapters are unlikely to be obtained easily. Numerical estimates of the persistence time distribution in such cases will, therefore, probably remain important. The insight obtained from the examination of simple models where analytical approximations are available is, therefore, very useful.

Finally, it is worth noting that while this chapter has only considered the first passage time when the absorbing boundary is constant the problem of the passage time to a level which varies with time has also received some attention in the literature. Examples include Favella *et al.* (1982) and Buonocore *et al.* (1990).



Chapter 3

Persistence time in models with density-independent vital rates

Introduction

This chapter investigates persistence in a simple linear model of population dynamics. Results for persistence time in similar models have previously been discussed by Capocelli & Ricciardi (1974), who consider a continuous time formalisation as opposed to the discrete time model used here, and both Tuljapurkar & Orzack (1980) and Lande & Orzack (1988) who consider structured (matrix) models. These discussions have focused on very small thresholds (usually one individual) in order to approximate extinction, rather than persistence above larger thresholds in the context of population management. The main shortcoming of the formalisation used here from an ecological viewpoint is the fact that it does not include any representation of natural population regulation (density-dependence) so unrealistically large populations may arise easily. The detection of density dependence in population census data is notoriously difficult and far from reliable (Gaston & Lawton 1987; Murdoch & Walde 1989). While more recent analyses (Turchin 1990, Woiwod & Hanski 1992, see also Godfray & Hassell 1992) have been more successful in finding evidence of density-dependence, it is rather more difficult to establish the appropriate functional form for its representation in a model. As such regulation can be introduced into a model in a variety of ways it is useful to have a good understanding of persistence in the linear model before looking at more complex situations.

Linear models of the form discussed below are quite likely to arise in applied modelling situations. In endangered (usually small) populations vital rates are likely to be density independent. In a management context it may, at times, be preferable to adopt a linear model for which parameters can be estimated, rather than a nonlinear model built on more less certain foundations. It has been pointed out many times (e.g. Murdoch 1970, Murdoch & Walde 1989) that experimental, rather than observational, studies are likely to be superior in providing information on density dependence and regulation of a population. Most populations of conservation interest are not, however, suited to experimental studies (as they are often rare and endangered) and must therefore rely on analysis of census data for information on their dynamics. Orzack & Tuljapurkar (1989) suggest that linear models can provide a "sufficient biological framework" when data regarding density dependence are lacking. The difficulty in detecting density dependence in population census data does not, of course, mean that such effects are not present and operating in the population. This must be borne in mind when assessing the results for population persistence in the linear model.

The basic model

The basis of this chapter is a multiplicative population model, in discrete time, with the general form

$$N_{t+1} = \lambda_t N_t = N_0 \prod_{i=0}^{t} \lambda_i \qquad [3.1]$$

where N_t is the size of the population, and λ_t is the multiplicative growth rate, at time *t*. This formalisation can, of course, include the case where the growth rate is a function of population size, but for the rest of this chapter only the case where λ_t is independent of population size will be considered. Further, it will be assumed that λ_t is an independent and identically distributed random variable (in other words, the λ_t are not autocorrelated and are drawn from a stationary distribution).

Population growth rate and distribution in the simple model

The model defined above is, of course, well known in the literature (see, for example, Lewontin & Cohen 1969). It is an obvious extension of the deterministic model, where the growth rate is constant, which results in exponential growth if $\lambda > 1$, exponential decline if $\lambda < 1$, and constant population size if $\lambda = 1$. Population growth rate in the stochastic model, however, is slightly more complicated and is best understood by first considering the asymptotic distribution of population size.

Taking logs in the model defined above and writing $\ln(N_t) = X_t$ and $\ln(\lambda_t) = r_t$ gives

$$X_{t+1} = X_t + r_t = \sum_{i=0}^{t} r_i + X_0 \qquad [3.2]$$

The term $\sum r_i$ is a sum of random variables with common mean and common, finite variance and will therefore (by the Central Limit Theorem) be asymptotically normally distributed. This leads to an asymptotically lognormal distribution for population size, N_t (Lewontin & Cohen 1969, Capocelli & Ricciardi 1974). There are parallel results for structured models which state that the total population size (i.e. summed over all age/stage classes, or some subset of the classes) will converge to a lognormal distribution (Tuljapurkar & Orzack 1980; Heyde & Cohen 1985).

The speed with which the distribution of population size converges to a lognormal distribution is, of course, important if use is to be made of these asymptotic results.

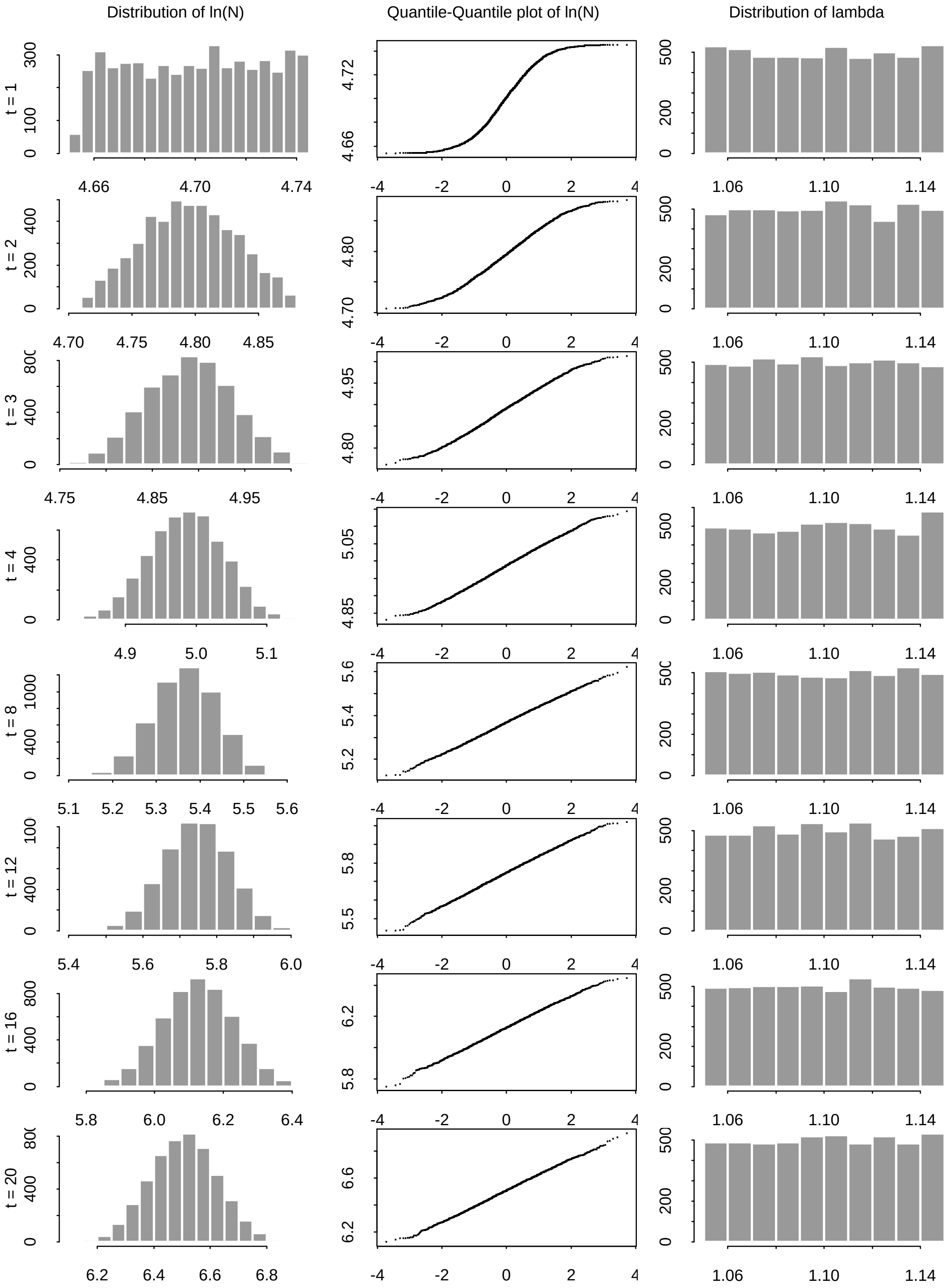


Figure 3.1. Illustration of the speed of convergence of the probability distribution of log population size in the simple model [3.1] to a normal distribution. The distribution of ln(N), quantile-quantile plots (Chambers *et al.* 1983) of ln(N) and the distribution of lambda are shown for time steps 1, 2, 3, 4, 8, 12, 16 and 20. The distributions were constructed from 5000 trials with N_0 = 100.

For the case where there is no autocorrelation in the random inputs the convergence is generally fast, (Tuljapurkar & Orzack 1980). The rapid convergence of the probability distribution of log population size to a normal distribution is illustrated in Fig. 3.1. Here 5000 replicates of the simple multiplicative population model [3.1] have been run, from a common initial state, for twenty time steps. The population growth rate is drawn from a uniform distribution which results in a uniform distribution of log population size at the first time step. However, this rapidly converges to a normal distribution, the visual impression of the histograms being confirmed by the straightening line in the quantile-quantile plots which plot the quantiles of the estimates distribution against those of the standard normal distribution (Chambers *et al.* 1983). Serial correlation in the multiplicative growth rate, λ, will make the convergence to a normal distribution slower (Lewontin & Cohen 1969).

The moments of the asymptotic distributions of population size and log population size at time *t* are related by the standard (and exact) formulae relating the mean and variance of a normal distribution and the 'associated' lognormal distribution (Johnson & Kotz, 1970, p.115):

$$\begin{aligned} \mathrm{E}(N_t) &= \exp\left(\mathrm{E}(X_t) + \frac{\mathrm{Var}(X_t)}{2}\right) \\ \mathrm{Var}(N_t) &= e^{2\mathrm{E}(X_t)} e^{\mathrm{Var}(X_t)} \left(e^{\mathrm{Var}(X_t)} - 1\right) \end{aligned} \qquad [3.3]$$

Note that Caswell's (1989, p.214, eqn. [8.38]) formula for the variance of the population size is different. A simple numerical experiment confirms that the form given here [3.3] is the correct form.

Returning now to the question of population growth rate, taking expectations in the model [3.1] yields

$$E(N_{t+1}) = N_0 E\left(\prod_{i=0}^{t} \lambda_i\right) = N_0 \bar{\lambda}^{t+1} \qquad [3.4]$$

(as the expectation of the product is the product of the expectation for an independent, identically distributed random variable). The expected population size thus grows exponentially at a rate given by the arithmetic mean of the growth rates. However, as shown above, population size, and the product of the multiplicative growth rate, is lognormally distributed. The expected population size is therefore greatly influenced by the very large population sizes occurring, with low probability, in the tail of the distribution. The modal population size is much less, corresponding to the much more likely values of the product of the growth rates. Lewontin & Cohen (1969) demonstrate (see also the clear discussion in Caswell, 1989, though note the errors in his equations [8.38] and [8.53] referred to elsewhere) that the ultimate fate of the population is determined by the expected value of the logarithm of the growth rates, $E\left[\ln\left(\lambda_t\right)\right]$. If $E\left[\ln\left(\lambda_t\right)\right]$ is less than zero then all populations tend to zero as time tends to infinity. The expected value of the logarithm of the growth rate is *not* the logarithm of the expectation of the growth rate, rather it is the logarithm of the *geometric* mean growth rate, i.e.:

$$E\left[\ln\left(\lambda_t\right)\right] = \ln\left(E\left[\left(\lambda_1\lambda_2\ldots\lambda_t\right)^{\frac{1}{t}}\right]\right) \qquad [3.5]$$

For Var(λ) > 0 the expected geometric mean is always less than the expected arithmetic mean of the multiplicative growth rate. It is therefore possible to have the situation where the expected population size grows to infinity but the probability of observing any population size other than ultimately tending to zero, is zero.

Thus, the appropriate measure of population growth is the expectation of the logarithm of the growth rate, $E\left[\ln\left(\lambda_t\right)\right]$ which describes the fate of the majority of realisations of [3.1], rather than the minority which dominate the value of $E[\lambda]$. Tuljapurkar & Orzack (1980) show that essentially the same result holds for the growth of total population size in structured populations. $E\left[\ln\left(\lambda_t\right)\right]$ will be referred to as the long run population growth rate and will generally be denoted by μ, and its variance denoted by σ^2.

Estimation of the long run growth rate

The persistence time results considered below are determined to a large extent by the long run growth rate, μ, and its variance, σ^2. Because the multiplicative growth rate can be distributed in many ways there is not a single, simple relationship between the mean and variance of the multiplicative growth rate for a time t, λ_t, and the mean and variance of the long run growth rate. Tuljapurkar (1982) and Lande & Orzack (1988) consider approximations for μ and σ^2 for structured populations. Dennis, Munholland & Scott (1991) consider maximum likelihood estimators for μ and σ^2 based on an observed time series of population censuses.

For the unstructured model considered here, an obvious candidate for the approximation of μ and σ^2 is based on the fact that the population size at a given time, and thus the product of growth rates to that point, is lognormally distributed. Rearrangement of the same formulae (Johnson & Kotz, 1970, p.115) that were used to relate the mean and variance of population size (at time *t*) to the mean and variance of log population size (eqn. [3.3]), suggests the approximations

$$\begin{aligned} \mu &\cong \ln\left(\bar{\lambda}\right) - \frac{\sigma^2}{2} \\ \sigma^2 &\cong \ln\left(1 + \frac{\mathrm{Var}(\lambda)}{\bar{\lambda}^2}\right) \end{aligned} \qquad [3.6]$$

Lewontin & Cohen (1969) suggest an alternative approximation for μ based on expansion of ln(λ) around $\bar{\lambda}$, the mean multiplicative growth rate:

$$\mu \cong \ln\left(\bar{\lambda}\right) - \frac{\mathrm{Var}(\lambda)}{2\bar{\lambda}^2} \qquad [3.7]$$

(note that this differs from Caswell's (1989, p. 216) eqn. [8.53] by the presence of the squared mean in the denominator. Lewontin & Cohen's form appears much more reasonable). They suggest no approximation for the variance of the long run growth rate. However, one of Lande & Orzack's (1988) approximations may be adapted to give

$$\sigma^2 \cong 2\left[\ln\left(\bar{\lambda}\right) - \mu\right] \qquad [3.8]$$

Table 3.1 compares these two approximations to the long run growth rate and its variance with numerical estimates, and exact results where possible, for several possible distributions of the multiplicative growth rate, λ. For the exponential and two state distributions of lambda the alternative approximations of [3.7] and [3.8] are slightly nearer the numerical (and, for the two state lambda, exact) values of the long run growth rate and its variance. However, the alternative approximation for λ lognormally distributed is wildly inaccurate.

This is obviously not the case for the lognormal approximation. The lognormal approximation performs more or less as well as the alternative approximations for the normal and uniformly distributed multiplicative growth rates. The lognormal approximation is therefore used throughout the thesis when it is necessary to obtain estimates of μ and σ^2 for given $\bar{\lambda}$ and Var(λ).

Both approximations considered here, and the numerical and exact results of Table 3.1, demonstrate the important feature of the long run growth rate which is that μ (= E[ln(λ)] is always less than ln(E[λ]) whenever Var(λ) > 0.

Table 3.1. Numerical estimates for μ and σ^2 for a variety of distributions of the multiplicative growth rate. Numerical estimates based on drawing 1.0E+6 sample multiplicative growth rates from the distributions specified and calculating $\mu = \mathrm{E}(\ln\lambda)$ and $\sigma^2 = \mathrm{Var}(\ln\lambda)$. "Lognormal" approximations from [3.6], "alternative" approximations from [3.7] and [3.8]. Exact μ and σ^2 for lognormally distributed λ from [3.3]. The "two state" distribution is Lewontin & Cohen's (1969) extreme example where λ can either take the value 0.5 or 1.7 with equal probability.

Multiplicative growth rate			Long run (i.e. logarithmic) growth rate							
			Exact		Numerical estimates		Approximations			
							lognormal		alternative	
distribution	$\bar{\lambda}$	Var(λ)	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2
uniform	1.00e+0	8.33e-2			-4.49e-2	9.45e-2	-4.00e-2	8.00e-2	-4.16e-2	8.33e-2
two state	1.10e+0	3.60e-1	-8.13e-2	3.74e-1	-8.05e-2	3.74e-1	-3.49e-2	2.60e-1	-5.35e-2	2.98e-1
normal	2.00e+1	9.00e+0			2.98e+0	2.39e-2	2.98e+0	2.23e-2	2.98e+0	2.25e-2
lognormal	2.44e+2	4.85e+8	1.00e+0	9.00e+0	1.00e+0	9.00e+0	1.00e+0	9.00e+0	-4.05e+3	8.10e+3
exponential	1.00e+0	1.00e+0			-5.76e-1	1.65e+0	-3.47e-1	6.93e-1	-5.00e-1	1.00e+0

Persistence time in the linear model

The logarithmic form of the model [3.2] in fact describes a generalised random walk which, as is well known, is approximated by a Wiener process in the continuous time limit (Cox & Miller 1965, p.235). Given the speed at which the log of population size converges to a normal distribution it is natural to consider whether the required persistence time results for the multiplicative population model [3.1] can be approximated by the first passage time distribution of the Wiener process, discussed in chapter 2. Using [2.24] it is possible to write the persistence time distribution for the simple multiplicative model as

$$g(t|N_0, N_a) = \frac{\ln(N_0 / N_a)}{\sigma\sqrt{2\pi t^3}} \exp\left(-\frac{\left(\ln(N_a / N_0) - \mu t\right)^2}{2\sigma^2 t} \right) \qquad [3.9]$$

where μ and σ^2 are the long run population growth rate and its variance respectively, N_0 is the population size at time zero and N_a is the lower threshold of interest. Fig. 3.2 compares the persistence time distribution given by [3.9] with that obtained

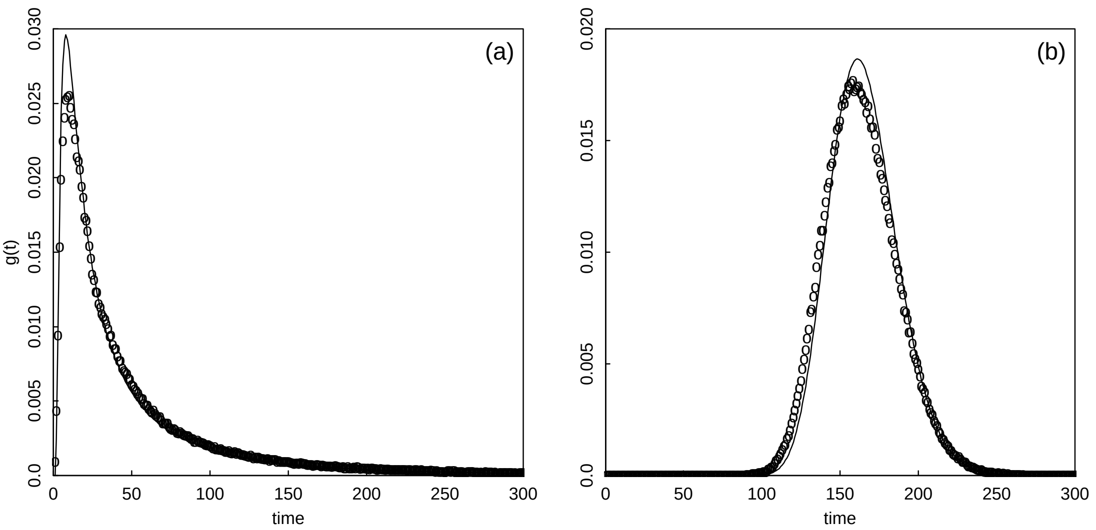


Figure 3.2. Simulated persistence time distributions for the simple multiplicative population model (points), and (lines) distributions from the Wiener process approximation [3.9]. The λ_t were drawn from a normal distribution and μ and σ estimated from [3.6], as discussed above. (a) N_0 = 8000, N_a = 3000, $\bar{\lambda}$ = 1, Var(λ) = 0.2; (b) N_0 = 6.0E+12, a = 3000, $\bar{\lambda}$ = 0.9, Var(λ) = 0.2.

numerically from simulation of the model [3.1] (the numerical methods used are discussed in appendix one). The fit is very good, the most noticeable deviation being the slight overestimation of absorption probability at the mode of the distribution. Lande & Orzack (1988) attribute this to the discrete nature of the model [3.1], which only allows crossing to the threshold at integer times, as opposed to the continuous nature of the Wiener process. If time steps less than one are used in the discrete model (i.e. euler integration) the fit does indeed improve: the scaling down of both time steps and changes in population size makes the Wiener approximation even more appropriate.

Expressions for various statistics of the persistence time of the model are also easily obtained from the results of chapter 2. Thus the conditional mean and mode are given by (where μ and σ are again given by [3.6]):

$$\text{mean} = \frac{\ln\left(N_0 / N_a\right)}{|\mu|} \tag{3.10}$$

$$\text{mode} = \begin{cases} \dfrac{\left(\ln\left[N_0 / N_a\right]\right)^2}{3\sigma^2} & (\mu = 0) \\[2ex] \dfrac{\left(N_0 / N_a\right)}{|\mu|}\left(1 + \dfrac{9\sigma^4}{4\mu^2\left(N_0 / N_a\right)^2}\right)^{\frac{1}{2}} - \dfrac{3\sigma^2}{2\mu^2} & (\mu \neq 0) \end{cases} \tag{3.11}$$

General features of the persistence time distribution

Fig 3.3 shows the shape of this persistence time distribution [3.9] for various sets of parameters (chosen more to illustrate the shape of the distribution rather than demonstrate any particular biological point). The distributions are unimodal and either skewed to the left (lines a, b, c) or almost symmetrical (lines d & a). Substitution in [2.30] gives an expression for ϕ, the parameter that controls the shape of the persistence time distribution:

$$\phi = \frac{|\mu| \ln\left(N_0 / N_a\right)}{\sigma^2} \qquad [3.12]$$

The values of ϕ for the curves of Fig. 3.3 are included with the modal and mean persistence time in Table 3.2. As expected from the discussion of the shape of the Wiener process passage time distribution in chapter 3, the more symmetrical curves (d and e in Fig. 3.3) have larger values of ϕ. It is clear from [3.12] and the example

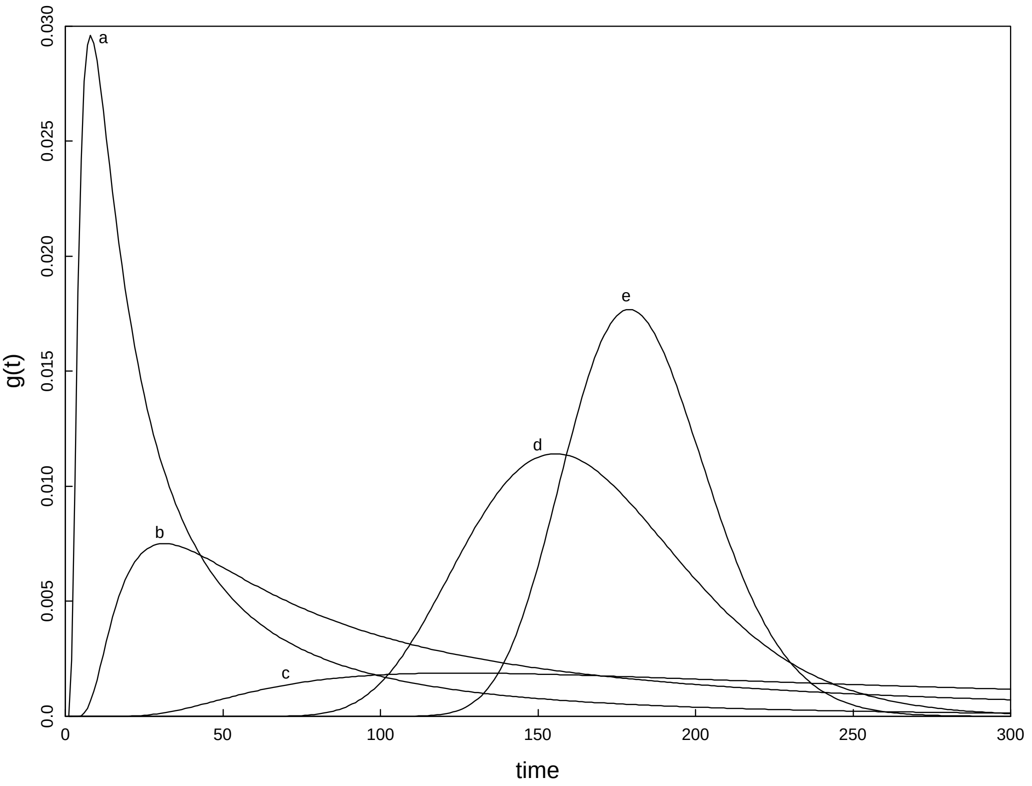


Figure 3.3. Examples of the distribution of persistence times (from eqn. [3.9]) for the simple population model [3.1] with λ_t a serially-independent, identically distributed random variable. The parameters used are in Table 3.2.

Table 3.2. Parameters used in eqn. [3.9] to produce the lines in Fig. 3.3. Also included are the expected and modal persistence times calculated from [3.10] and [3.11] respectively (both given to two decimal places).

	N_0	N_a	$\bar{\lambda}$	Var(λ)	$E(T)$	modal T	ϕ
a	8.0E+3	3.0E+3	1	0.04	50.02	7.97	0.49
b	8.0E+3	3.0E+3	1	0.01	197.15	31.41	0.49
c	8.0E+3	3.0E+3	1	0.0025	785.64	125.17	0.49
d	6.0E+8	3.0E+3	0.95	0.04	167.26	155.49	20.54
e	6.0E+13	3.0E+3	0.9	0.04	183.21	178.95	63.70

parameters (Table 3.2) producing the example curves in Fig. 3.3 that, in a population context, the vast majority of likely parameters will lead to a skewed persistence time distribution, with a tail of long persistence times arising with low probability.

Fig. 3.3 and Table 3.2 illustrate a further feature of the persistence time that is of some importance, namely that the long tail in some of the more skewed distributions results in large expected persistence times. Thus the expected persistence times for parameter sets (b) and (c) exceed the expected times for sets (d) and (e). However the modal passage times for (d) and (e) exceed those of (b) and (c).

This feature has some consequences for the use of passage time distributions in the evaluation of population models. In particular it would probably be unsatisfactory to conclude (on the basis of the expected persistence time) that a population described by a model giving rise to distribution (b) in Fig. 3.3 would be likely to persist longer than that a population with persistence time from distribution (e). While a few realisations of the process with persistence time distribution (b) will persist for considerably longer than virtually all realisations of process (e), the majority of realisations of (b) will reach the lower threshold before those of process (e). Given that we will generally be interested in the fate of a single population (i.e. a single realisation) the mode is likely to be a better indicator of persistence above the threshold. This problem is investigated further in Fig. 3.4 where the cumulative persistence time distributions (i.e. the probability that absorption has taken place by time t) are shown for two of the curves specified by in Table 3.2. The cumulative

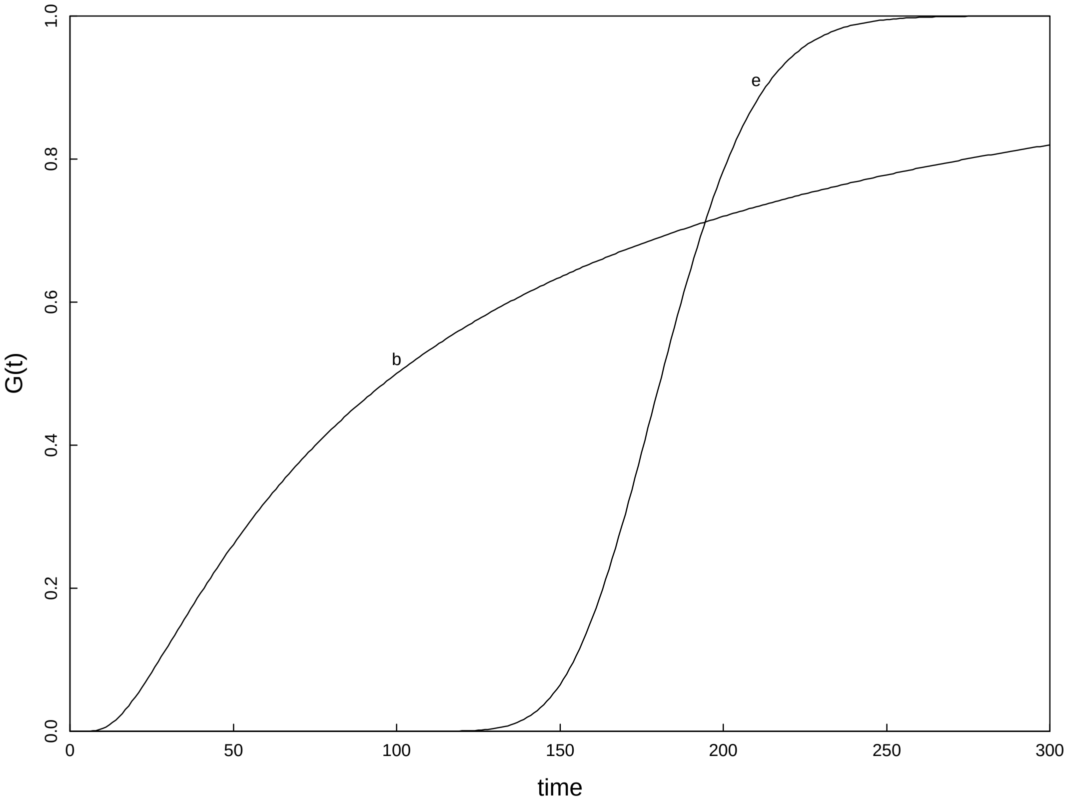


Figure 3.4. Probability of absorption by time *t*, *G*(*t*), for the parameter sets (b) and (e) of Table 3.2.

probability for (b) begins to accumulate sooner than that of (e), but (e) overtakes (b) around $t = 200$.

There is, it appears, no "perfect" summary statistic for comparing persistence time distributions for different parameter sets or different models. However it will generally be convenient to use some summary statistic rather than continually compare pictures of distributions. The preceding discussion illustrates the need to choose the statistic with some care, and to investigate other features of the distribution where possible. At times this will mean resorting to numerical estimates of the persistence time distribution due to the fact that, as emphasised in chapter 2, closed form expressions for more complex models are difficult to obtain.

Determinants of persistence time

In this section the effect of varying the parameters of the simple multiplicative model on the persistence time is examined. While various authors (Capocelli & Ricciardi 1974; Lande & Orzack 1988) have considered the persistence time in terms of the long run growth rate, there are advantages to considering the model [3.1] in the actual terms in which it is conceived. In particular it is useful to distinguish what Shaffer (1981) terms the systematic pressures and stochastic perturbations facing a population. A multiplicative growth rate less than one could be termed a systematic pressure leading to a population reaching some low threshold size, while the variance in this growth rate represent the stochastic perturbations. The long run growth rate, μ , in contrast is a measure which incorporates the effects of both systematic pressure and environmental stochasticity. While this is useful in some circumstances, it may also lead to some confusion. Lande & Orzack state, for instance, that "the mean time to extinction....depends on the infinitesimal variance, σ^2, only through its effect on the long run growth rate of the population, μ" (see eqns. [3.6] and [3.10]). While this statement is undeniably true it may serve to detract attention from the important role that environmental variance (introduced in the multiplicative growth rate and greatly affecting σ^2) actually plays in determining persistence times. Stacey & Taper (1992) are apparently unaware of the distinction between the long run growth rate and the multiplicative growth rate and thus rediscover the fact that environmental variance leads to all realisations of their model (which is discussed further at the end of chapter 4) reaching a lower threshold, even when $\lambda = 1$.

The effects of three variables are of interest: the multiplicative growth rate, $\bar{\lambda}$, and its variance, Var(λ), and the ratio of initial population size, N_0, to the threshold level N_a. It would seem natural to suggest that for constant distance between the initial population size and the lower threshold, $(N_0 - N_a)$, the persistence time distribution should be the same. This is not, in fact, the case. The lognormal distribution of population size means that the persistence time distribution from, say, 100000 to 97000 individuals is not the same as the distribution from 8000 to 5000 individuals. This is illustrated in Fig. 3.5. From [3.9] it can be seen that the appropriate measure is N_0/N_a.

The probability of ultimately reaching the threshold

As noted in chapter 2 in the discussion of the first passage time of the Wiener process with a single absorbing barrier, there are cases where ultimate (i.e. as $t \to \infty$) absorption is not certain. Similarly, for the simple multiplicative population model there are cases where the population growth rate is sufficiently large (and the variation in this rate suitably small) that at least some of the realisations of the model will not ever reach the threshold level. By making the appropriate substitutions in

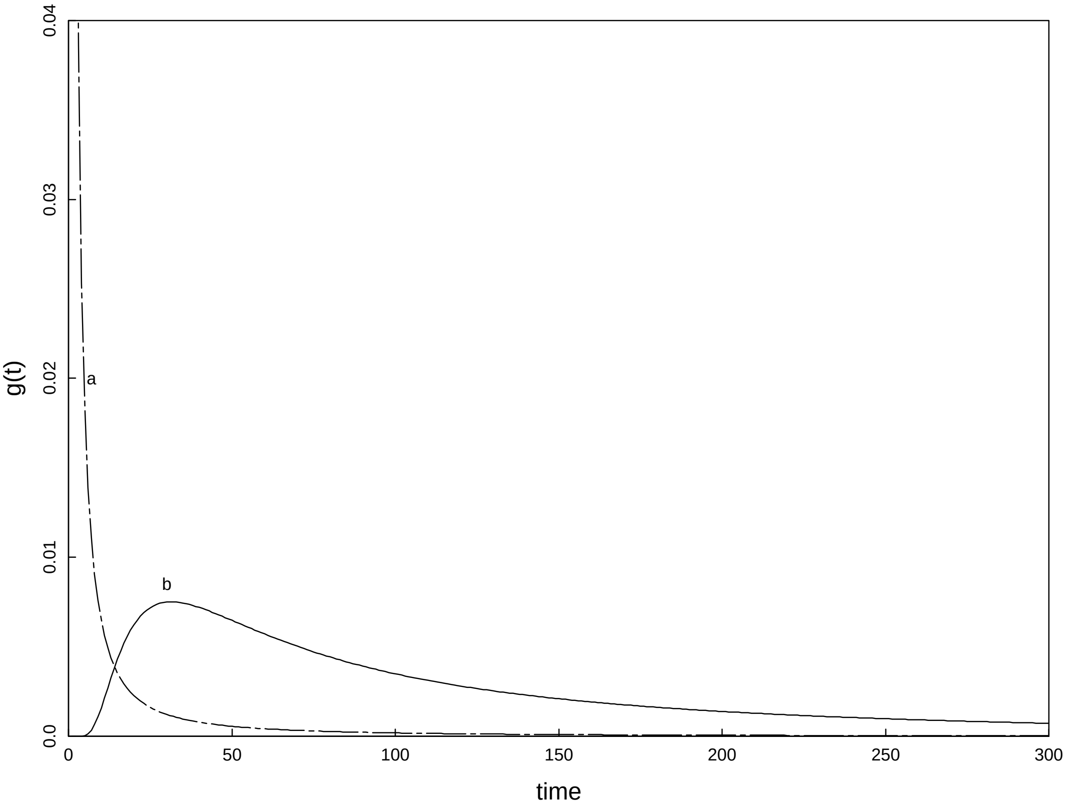


Figure 3.5. Persistence time distributions (calculated using eqn. [3.9]) for (a) N_0 = 100000, N_a = 97000, (b) N_0 = 8000, N_a = 5000, with $\overline{\lambda}$ = 1 and Var(λ) = 0.01 in both cases. Despite the fact that (N_0 − N_a) = 3000 in both (a) and (b) the lognormal distribution of population size means that these distributions are not the same.

equation [2.25] expressions for the probability of ultimately reaching the threshold are obtained:

$$G\left(\infty \middle| N_0, N_a\right) = \begin{cases} 1 & (\mu \le 0) \\ \exp\left(-\dfrac{2\mu}{\sigma^2}\ln\left(N_0 / N_a\right)\right) & (\mu > 0) \end{cases} \qquad [3.13]$$

where, as before μ and σ are given by [3.6]. Thus, where the long run population growth rate, μ, is positive, there is the potential for at least some of the realisations to persist above the threshold indefinitely.

Fig. 3.6 illustrates (for various values of Var(λ)) the effect of increasing $\overline{\lambda}$ on the probability that the threshold level is eventually reached. Especially for lower values of Var(λ) the transition from certain absorption at the threshold to almost zero probability of ultimately reaching the threshold takes place over a remarkably small

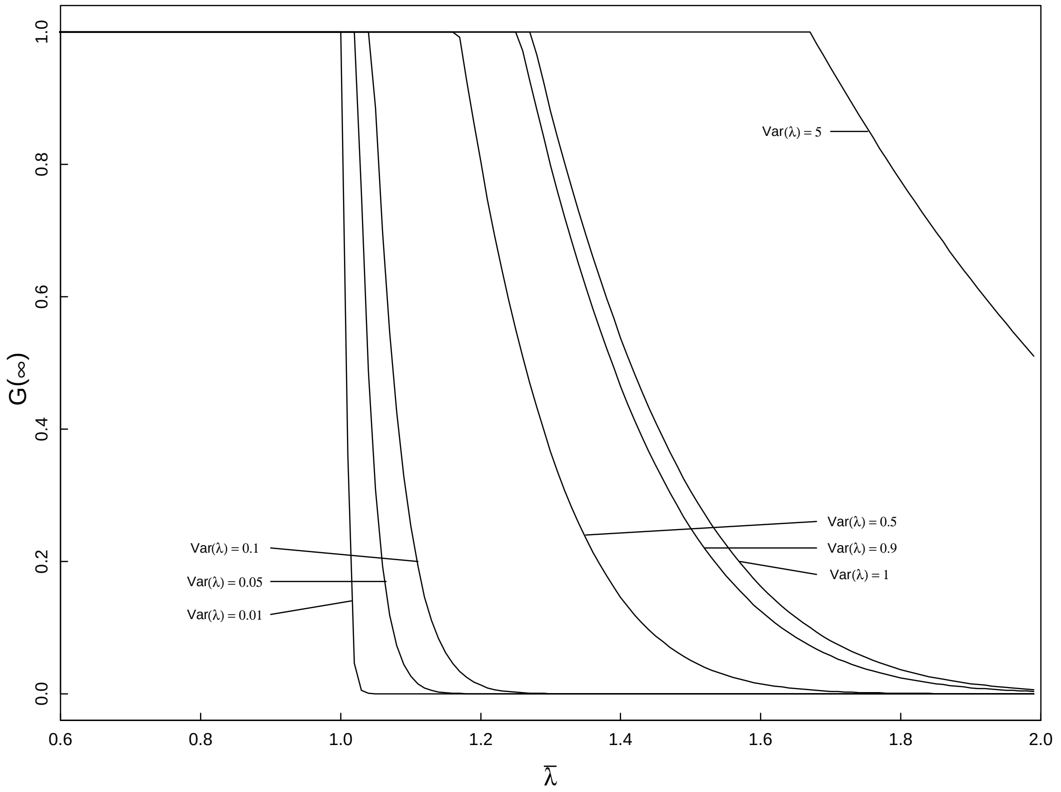


Figure 3.6 The effect on $G(\infty)$ of varying $\bar{\lambda}$ for various values of Var(λ). $N_0 = 8000$, and $N_a = 3000$.

range of $\bar{\lambda}$. Fig. 3.7 shows the mean and modal persistence times as $\bar{\lambda}$ varies in this transition zone. Both mean and modal persistence times actually decrease as $\bar{\lambda}$ increases. In isolation this is a slightly surprising result. However this must be seen in the context of rapidly decreasing probability of absorption, and the fact that we are considering the mean *conditional* on the threshold actually being reached. As $\bar{\lambda}$ increases the only realisations that reach the threshold are those that have a downwards fluctuation while the population size is still very near the initial value. As the population grows quickly from this level, later absorption is very unlikely. Thus the decreasing (conditional) mean and modal persistence times are reflecting the fact that the chance of the threshold being reached is falling, and those realisations that do reach the threshold are mainly those that happen to fluctuate downwards when t is small.

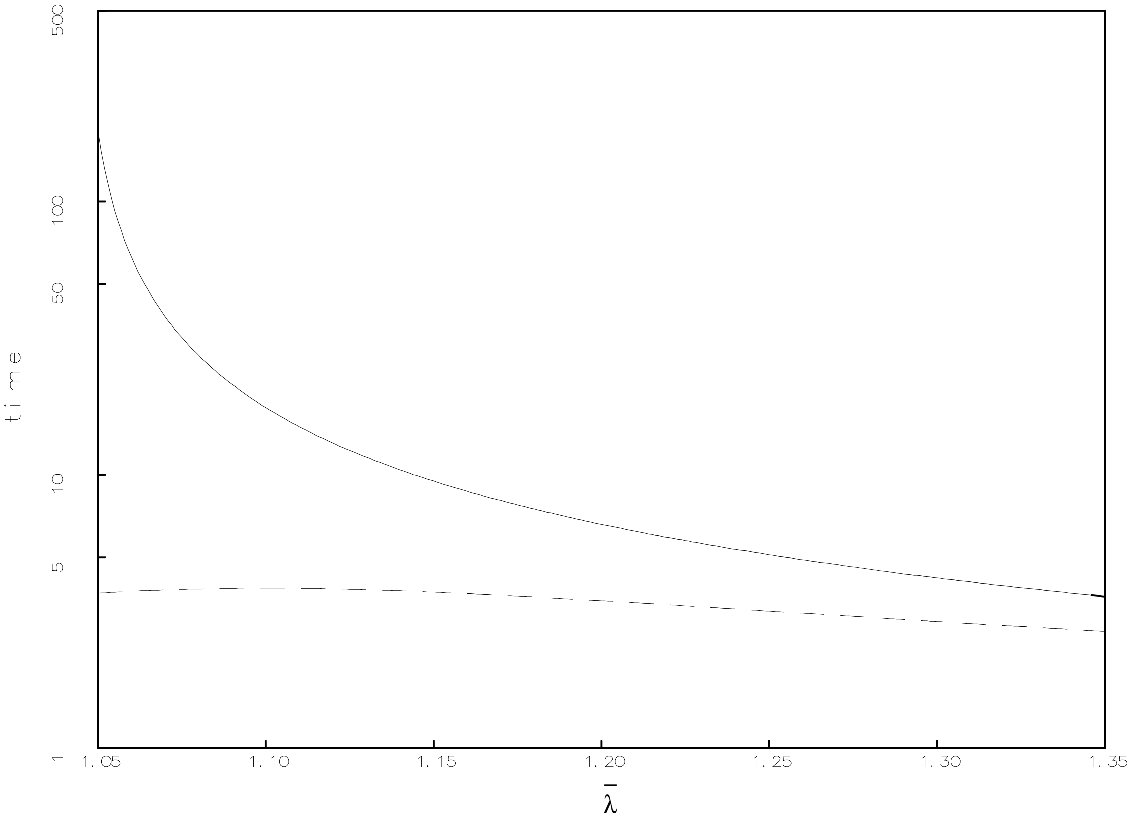


Figure 3.7. The change in conditional mean (—) and modal (--) persistence time as $\bar{\lambda}$ is varied through values which produce the transition from $G(\infty) = 1$ to $G(\infty) \approx 0$. [Var(λ) = 0.1, $N_0 = 8000$, and $N_a = 3000$].

Thus the first stage in a quantitative evaluation of the effect on persistence of a change in the parameters of the simple model [3.1] is to check whether the probability of ultimate absorption is changed. For the rest of this section the confounding effect of changes in $G(\infty)$ is avoided by considering only cases where reaching the threshold is certain, given sufficient time [$G(\infty) = 1$]. The effect of varying $\bar{\lambda}$, Var(λ), and N_0/N_a on the persistence time is investigated. This is not to imply that the distribution of persistence times is not of interest where $G(\infty) < 1$: indeed the behaviour of the model in finite time is still likely to be important. However, interest here is in the general effects of a change in parameters on modal and mean persistence times and comparison is really only relevant if $G(\infty)$ is constant. The only level at which $G(\infty)$ can easily be fixed is one.

In Fig. 3.8 Var(λ), N_0, and N_a are constant while $\bar{\lambda}$ is varied through a range which mostly produces certain ultimate absorption ($G(\infty) = 1$). The transition to $G(\infty) < 1$ is marked by the decline following the sharp peak in the conditional mean persistence

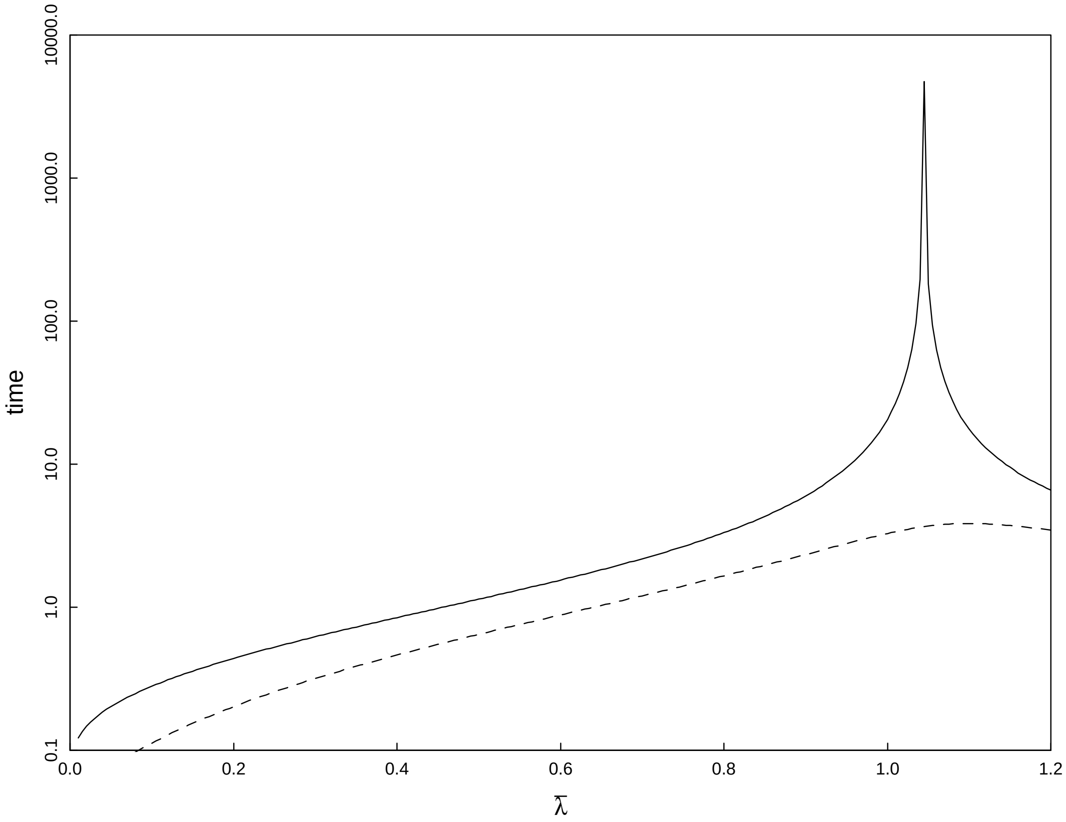


Figure 3.8. The effect of varying $\bar{\lambda}$ on the conditional mean (—) and modal (--) persistence time with Var(λ) = 0.1, N_0 = 8000, and N_a = 3000. Note that the ordinate is plotted logarithmically.

time. This figure illustrates the fact, apparent from eqn [3.10], and emphasised by Lande & Orzack (1988), that the conditional distribution of mean persistence times is symmetrical about $\mu = 0$. The conditional mean (and the conditional distribution of persistence times) thus depends on the absolute magnitude of the long run growth rate, not whether it is positive or negative.

For smaller values of $\bar{\lambda}$ the conditional mean and modal persistence times are similar in magnitude and increase steadily with increasing $\bar{\lambda}$. However for larger values of $\bar{\lambda}$ the mean increases much more rapidly than the mode. This coincides with the long run population growth rate, μ, approaching zero. The rapid increase in mean persistence time is due to the fact that, despite the long run growth rate being negative and ultimate absorption certain, a few realisations continue for very long times before reaching the lower threshold. Thus some populations described by the simple multiplicative model may, in fact, persist for a long time despite negative long term growth rates. However the majority of realisations continue to reach the

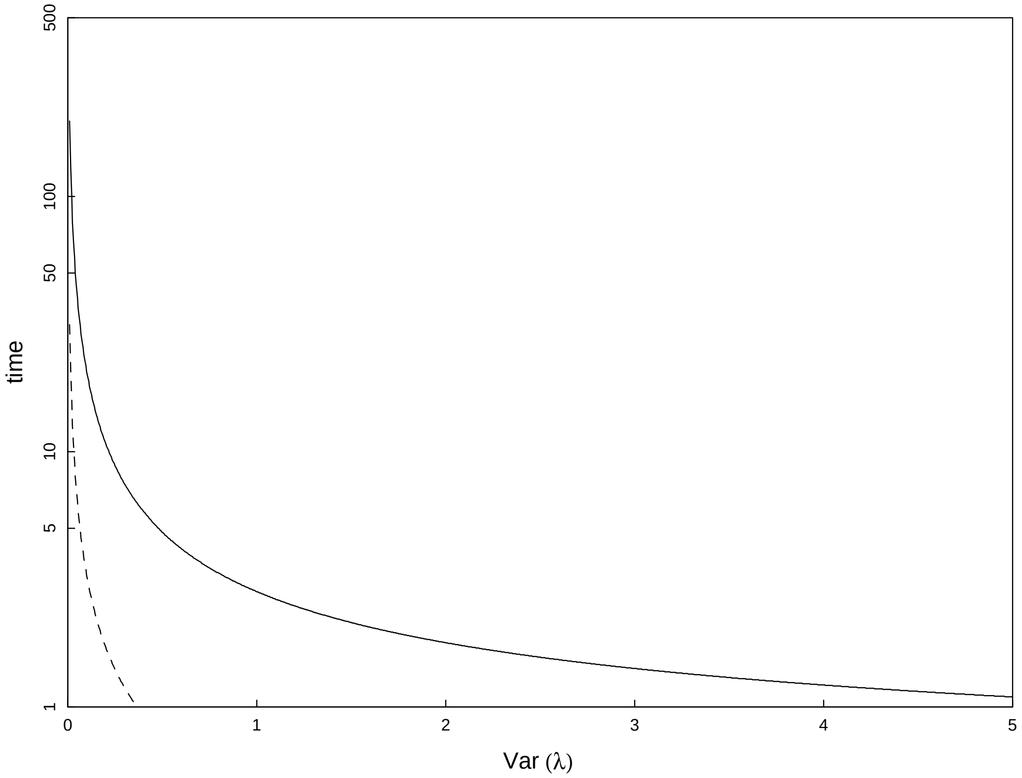


Figure 3.9. The effect of varying Var(λ) on the conditional mean (—) and modal (--) persistence time with $\bar{\lambda} = 1$, $N_0 = 8000$, and $N_a = 3000$.

threshold within a reasonably short time: thus the modal persistence time does not increase nearly so rapidly as the mean as $\bar{\lambda}$ is increased.

Fig. 3.9 investigates the effect of changing Var(λ) on the mean and modal persistence times. The relationship is simple – increasing the variance of the multiplicative population growth rate rapidly decreases both the modal and conditional mean persistence times. The modal persistence time decreases rather more rapidly than the mean as Var(λ) is increased. Again this is due to the fact that some realisations may persist for long times, thus increasing the mean.

Fig. 3.10 illustrates the effect of varying the ratio of initial population size to threshold population size (N_0/N_a) on the mean and modal persistence time, for a given mean and variance of the multiplicative growth rate. Unsurprisingly, increasing this ratio increases both the mean and modal persistence times. Note, however the abscissa is logarithmic. Thus, as a result of the logarithmic distribution of population

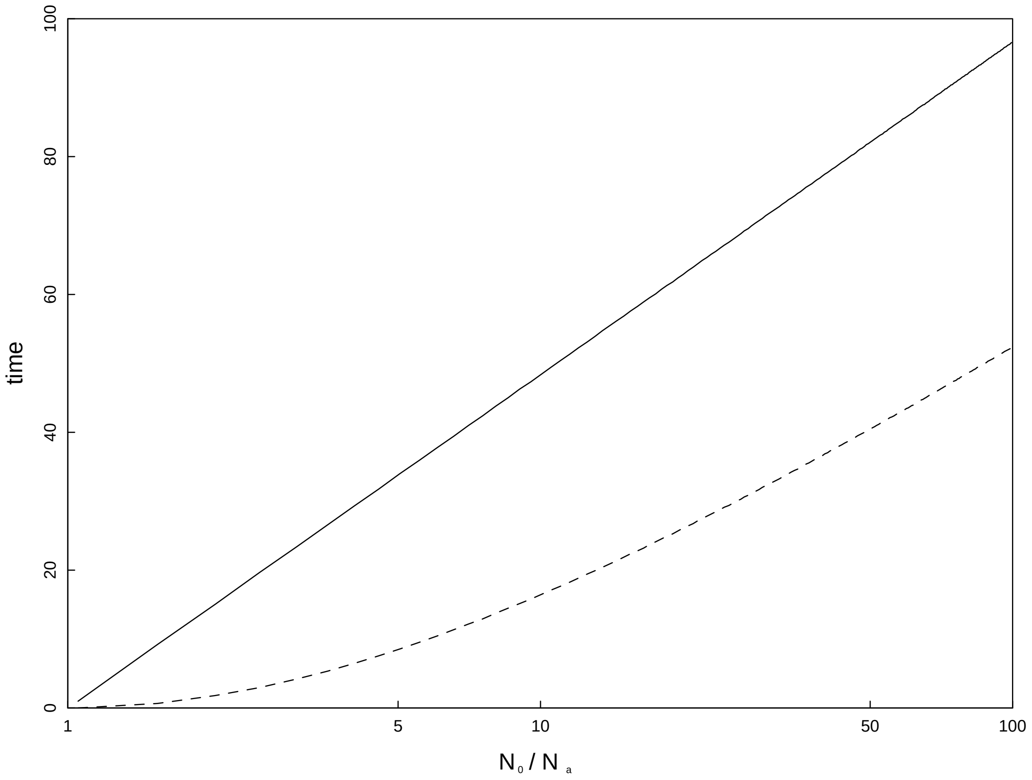


Figure 3.10. The effect of varying the ratio N_0/N_a on the conditional mean (—) and modal (---) persistence time with $\bar{\lambda} = 1$, Var(λ) = 0.1.

size, mean persistence time increases only logarithmically with increases in the ratio of initial population to threshold population. The modal persistence time increases even less rapidly.

Discussion

The persistence time distribution of the simple linear model has several lessons for the use of persistence time as a viability criterion in the comparison of management strategies in stochastic models. Firstly, it is important to recognise that the distribution may be highly skewed. Thus, while the majority of realisations of the model may reach the lower threshold in a relatively short time, a small number may have extremely long persistence times leading to large mean persistence times. Where that fate of a single population is of interest the modal value is more likely to be useful. However, where the probability of ultimate absorption is constant, the modal and mean persistence time generally show a similarly shaped response when a single parameter is varied. The exception to this is the behaviour of the mean in the region where the long run growth rate, μ, is near zero. In such cases mean persistence time is considerably greater than the most likely persistence time. This, of course, is of particular interest in conservation problems where populations may be on the "edge of viability" with a long run growth rate near zero. A further lesson for the use of persistence time as a viability criterion is that the ultimate probability of reaching the threshold may have to be considered in addition to the change in either modal, or mean, persistence time.

Shaffer (1987) suggests that average persistence times will increase linearly with increasing population size under the effects of environmental stochasticity. Fig. 3.10 suggests, that for the linear model considered here, the picture is in fact rather different. While both mean and modal persistence times do increase as the initial population size is increased, the rate of this increase is logarithmic. Increased population size may not, therefore, be as good a route to increased persistence times as was once assumed.

One area of applied biology where the relationship between initial population size and persistence time may be of great importance is in the field of biological control. The size of the initial release of the control species is likely to be one of the main financial implications for any biological control scheme, whereas persistence time of the vector in the environment into which it is released is likely to be one of the main determinants of the scheme's success. It is conceivable that any exotic species released into an ecosystem in considerable numbers will be described quite well by a simple linear model. For example, it is likely to take some time for predator populations to adapt to the biological control species as a suitable prey item. The relationship between initial population size and likely persistence time of Fig 3.10 may, therefore, provide a useful basis for a form of cost-benefit analysis when making the decision about initial release size.

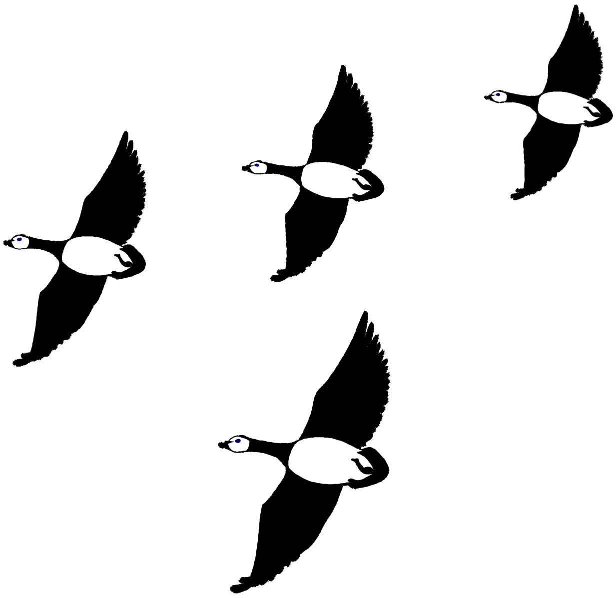
Lande & Orzack (1988) make the point that mean persistence time, for a given threshold and initial population size, is a function only of the long run population growth rate, μ. However this growth rate is heavily influenced by the magnitude of the environmental variance. As Fig. 3.9 shows, increasing the variance of the multiplicative growth rate, Var(λ), results in substantial decreases in both mean and modal persistence times in the linear model. Any impact envisaged on a population must, therefore, consider not only its affect on the growth rate, λ, but also its variance.

In the introduction to this chapter it was suggested that one problem with the linear model considered here is that it fails to represent density dependent population regulation. However, this does give the opportunity to evaluate persistence time in the absence of such regulation. Sinclair (1989), in reviewing population regulation in animals, notes that "... the most contentious aspect of Andrewartha & Birch's theory is that populations could persist without regulation. It is generally recognised that such populations would show a random walk through time and eventually go extinct ..". Thus, the very fact that populations are observed to persist is often used as an argument for the necessity of density dependent regulation. However, as noted above, the logarithm of population size described by the linear model is, in fact, a generalised random walk. The persistence time distribution for the linear model shows that (with low probability) some realisations may actually persist for very long times, despite the lack of density dependent regulation. Indeed eqn. [3.13] demonstrates that, if the long run population growth rate is positive, there is actually a finite chance that the population will persist indefinitely above some lower threshold. Fig. 3.8 demonstrated that, even when ultimately reaching the lower threshold is certain ($\mu \leq 0$), the mean persistence time may be extremely long and, indeed, when the long run growth rate, μ, is zero the mean persistence time is actually infinite.

Sinclair (1989) goes on to quote Strong (1984) who asserts that extinction in random walk models is too frequent to mimic the behaviour of real populations. Sinclair points out that this assertion is actually rather difficult to test. However, it is interesting to note that recent studies of the persistence time of island populations (Schoener & Spiller 1987) suggest that short persistence times are quite common, and *local* extinction rather frequent. The persistence time distribution of the linear model, with a tail of very long persistence times indicates a mechanism by which a fragmented population may persist for much longer than any one of its component sub-populations. If the sub-populations vary in size, or experience locally variable environments, then a range of persistence times will result. If the sub-populations are sufficiently connected such that recolonisation is possible, then local extinction may be frequent while, overall, the population continues to persist. The effect of fragmented populations is receiving increasing attention in the ecological literature as the concept of "metapopulation" dynamics gains strength (see, for instance, Gilpin & Hanski 1991).

The discussion above illustrates the fact that long persistence times may result in populations without density dependent regulation. This is not, however, to suggest that such regulation is either absent or unimportant. Indeed as longer population census time series, and improved statistical methods, become available, the detection of density dependence in real world data becomes more frequent (Godfray & Hassell 1992; Woiwod & Hanski 1992). As evidence of the importance of non-linearities in the dynamics of populations accumulates from real data, proponents of density dependence can perhaps put aside the well worn, but false, argument that a "random walking" population must *necessarily* go extinct. Part of the confusion which arises can be traced to the use of terms such as density dependence, regulation and persistence in an effectively interchangeable manner. A recent discussion of the problems of terminology in this area is Hanski (1990).

The persistence time distribution for the simple linear stochastic population model thus results in insight into various areas of ecological theory as well as providing baseline results for comparison with persistence in more complex models.



Chapter 4

The linear model with an upper limit to population size

Introduction

The simple multiplicative population model considered in the previous chapter had a population growth rate that was independent of population size. While this model may be appropriate in certain circumstances, it suffers from the rather unrealistic feature that infinitely large populations may arise. One way to avoid this is to incorporate explicit dependence of growth rate on population size. However, this could be done in a number of ways and, in the context of models for population management, it may not be clear which functional form should be used. An alternative approach, which prevents the problem of infinite populations while avoiding the many complexities associated with non-linear stochastic models, is to simply fix a hard upper limit to population size. While this is chosen largely for computational ease in order to give insight into the effects of a "first approximation" to population regulation, a hard upper limit to population size is not totally without a biological basis. For instance, an absolute maximum population may arise as an extreme form of contest competition (Varley, Gradwell & Hassell 1973) where, in a population below the maximum size, all individuals get sufficient resources, while any excess recruitment of individuals results in their rapid death (rather than their taking a share of the resources, thus reducing the *per capita* resource use by the population). An example of this is competition for breeding territories as there is likely to be some limit to the number of territories into which a given area can be divided (Stacey & Taper 1992). An upper limit to population size, with a region below this limit where fluctuations in size are produced purely by environmental variation, also has some similarities to Strong's (1986a,b) concept of density-vague regulation. Strong (1986a) considers the case of populations with a density-vague region below some ceiling which may be imposed through resource depletion, natural enemies or emigration. The ceilings considered by Strong are rather more general than the upper limit considered in this chapter: Strong's (1986a, Fig. 15.4) illustrates ceilings which vary through time, a situation which complicates the mathematics of the first passage time immensely.

The model

The model is essentially the same as that used in chapter 3: an unstructured population model with an independent and identically distributed multiplicative growth rate. However, in addition we now define a level, N_b, such that $N_t \le N_b$ for all t:

$$N_{t+1} = \begin{cases} \lambda_t N_t & \text{if } \lambda_t N_t \le N_b \\ N_b & \text{otherwise} \end{cases} \tag{4.1}$$

Persistence time

In chapter 3 the logarithm of population size was approximated as a Wiener process and the Wiener process first passage time distribution was found to closely approximate the persistence time distribution of the model. The upper limit to population size, N_b, is equivalent to imposing an upper reflecting barrier at $\ln(N_b)$ on the Wiener process approximation to log population size. Thus, by referring back to chapter 2, an approximate expression for the persistence time distribution for the simple multiplicative model with a hard upper bound can be found.

If the long run population growth rate, μ, equals zero then the persistence time probability density function is given (from [2.44]) by

$$g\left(t \middle| N_0, N_a, N_b\right) = \frac{\pi}{\left(\ln\left(N_b / N_a\right) / \sigma\right)^2} \sum_{n=0}^{\infty} \left[(-1)^n \left(n + \tfrac{1}{2}\right) \times \cos\left(\left(n + \tfrac{1}{2}\right) \frac{\pi \ln\left(N_0 / N_b\right)}{\ln\left(N_b / N_a\right)} \right) \exp\left(\frac{-\left(n + \tfrac{1}{2}\right)^2 \pi^2 t}{2\left(\ln\left(N_b / N_a\right) / \sigma\right)^2} \right) \right] \tag{4.2}$$

where μ and σ are given by [3.6].

If $\mu \neq 0$ then, from [2.41],

$$\begin{aligned} g\left(t \middle| N_0, N_a, N_b\right) = {} & \exp\left(-\frac{\mu^2 t}{2\sigma^2} - \frac{\mu}{\sigma^2} \ln\left(\frac{N_0}{N_a}\right) \right) \frac{\sigma^2}{\ln\left(N_b / N_a\right)} \\ & \times \sum_{n=1}^{\infty} \left[\exp\left(-\frac{\lambda_n^2 \sigma^2 t}{2} \right) \frac{\lambda_n \sin\left(\lambda_n \ln\left(N_b / N_a\right)\right)}{1 - \dfrac{\mu}{\lambda_n^2 \ln\left(N_b / N_a\right) \sigma^2} \sin^2\left(\lambda_n \ln\left(N_b / N_a\right)\right)} \right. \\ & \left. \times Y_n \ln\left(\frac{N_b}{N_0}\right) \right] + \exp\left(-\frac{\mu^2 t}{2\sigma^2} - \frac{\mu}{\sigma^2} \ln\left(\frac{N_0}{N_a}\right) \right) \frac{\sigma^2}{\ln\left(N_b / N_a\right)} k \end{aligned} \tag{4.3}$$

where $Y_n(x)$ is given by [2.36], the λ_n satisfy

$$\tan\left(\lambda_n \ln\left(N_b / N_a\right)\right) = \frac{\lambda_n \sigma^2}{\mu} \qquad [4.4]$$

such that $0 < \lambda_1 < \lambda_2 < \ldots$, and

$$k = \begin{cases} 0 & \text{if } \dfrac{\mu(b-a)}{\sigma^2} < 1 \\[2em] \dfrac{3\ln\left(N_0 / N_a\right)}{\ln\left(N_b / N_a\right)^2} & \text{if } \dfrac{\mu(b-a)}{\sigma^2} = 1 \\[2em] \exp\left(-\dfrac{q^2\sigma^2 t}{2}\right) V\left(\ln\left(N_b / N_0\right)\right) \\ \quad \times \dfrac{2q\sinh\left(q\ln\left(N_b / N_a\right)\right)}{-1+\sinh^2\left(q\ln\left(N_b / N_a\right)\right)\mu / \left(\sigma^2 \ln\left(N_b / N_a\right) q^2\right)} & \text{if } \dfrac{\mu(b-a)}{\sigma^2} > 1 \end{cases} \qquad [4.5]$$

where $V(x)$ is given by [2.39], and q is the positive solution of

$$\tanh\left(q\ln\left(N_b / N_a\right)\right) = \frac{q\sigma^2}{\mu} \qquad [4.6]$$

The expected persistence time is given by

$$E\left(T \middle| N_0, N_a, N_b\right) = \begin{cases} \dfrac{\sigma^2}{2\mu^2} \exp\left(\dfrac{2\mu\ln\left(N_b / N_a\right)}{\sigma^2}\right) \\ \quad \times \left[1 - \exp\left(-\dfrac{2\mu\ln\left(N_0 / N_a\right)}{\sigma^2}\right) \right. \\ \quad \left. - \dfrac{2\mu\ln\left(N_0 / N_a\right)}{\sigma^2} \exp\left(-\dfrac{2\mu\ln\left(N_b / N_a\right)}{\sigma^2}\right)\right] & \mu \neq 0 \\[3em] \dfrac{\ln\left(N_0 / N_a\right)\ln\left(N_b^2 / N_a N_0\right)}{\sigma^2} & \mu = 0 \end{cases} \qquad [4.7]$$

Features of the persistence time distribution

Unlike the model of chapter 3, where populations with a positive long run growth rate had a chance of never reaching the lower threshold, a finite upper limit to population size means that reaching some low level is ultimately certain. Fig. 4.1 investigates the change in persistence time distribution resulting from the imposition of an upper bound for parameters that give different values of m $\left(=\sigma^2 \big/ \left[\mu \ln\left(N_b / N_a\right)\right]\right)$, which relates to different forms of the persistence time distribution (see Fig. 2.2). The parameters used are given in Table 4.1.

The case $m < 0$ can obviously only come about when the long run growth rate, μ, is negative. It is not surprising (given that the population is naturally decreasing) that in this situation the distribution of persistence times (Fig. 4.1b) is similar for the unbounded model of chapter 3 and the model with an upper limit [4.1]. There are, however, slight differences, most notably the fact that the distribution of persistence times in the unbounded model has a longer tail. This is due to the fact that even a population with μ negative may occasionally fluctuate to large population sizes and

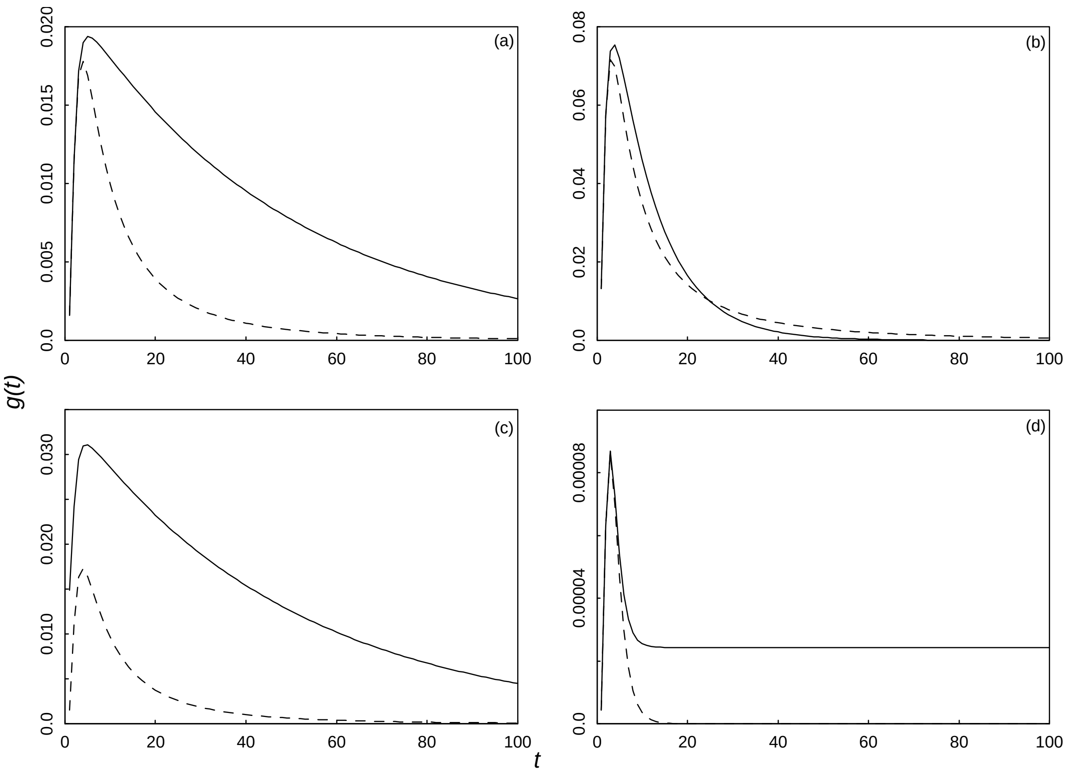


Figure 4.1. Persistence time distributions for the linear model with [4.1] (——) and without [3.9] (– – –) a hard upper bound to population size. The parameters used are in Table 4.1.

Table 4.1. Parameters used in equations [4.3] and [3.9] to produce the persistence time distributions of Fig. 4.1.

	$\bar{\lambda}$	Var(λ)	N_0	N_a	N_b	μ	σ	m
(a)	1.1	0.1	8000	3000	12000	0.056	0.28	1.03
(b)	1.0	0.1	8000	3000	12000	–0.048	0.31	–1.44
(c)	1.10155	0.09999	8000	3000	12000	0.057	0.28	1.00
(d)	1.3	0.1	8000	3000	12000	0.23	0.24	0.18

therefore achieve a long persitence time. This possibility is prevented in the model with the upper limit to population size.

The cases $m > 1$ and $m = 1$ (Fig. 4.1a,c) arise where μ is moderate relative to the standard deviation in the growth rate. In these cases the addition of an upper limit to population size greatly raises the tail of the persistence time distribution relative to that of the unrestricted model. Whereas the positive long run growth rate in these cases allows some realisations of the unrestricted model to continue growing and never reach the threshold, in the restricted model all realisations reach the threshold. The area under the persistence time distribution of the restricted model is thus noticeably greater. When $0 < m < 1$ (i.e. the long run growth rate is large relative to its standard deviation and the distance between the upper limit and lower threshold) the situation is slightly different (Fig. 4.1d). The initial part of the persistence time distribution of the restricted model is very close to that of the unrestricted model; the main difference is the raised tail of the distribution for the restricted model. In this case the probability of reaching the threshold at any particular time is very small - in the restricted model the raised tail declines only very slowly, such that a small probability of reaching the threshold continues to long times.

The observation that, for μ strongly positive, the greatest difference between the persistence time distributions of the restricted and unrestricted models are in the *tail* of the distribution, is important. While the probability of *ultimately* reaching the threshold in the restricted model is one, much of this probability could represent realisations reaching the threshold only at very long times. Fig. 4.2 considers the

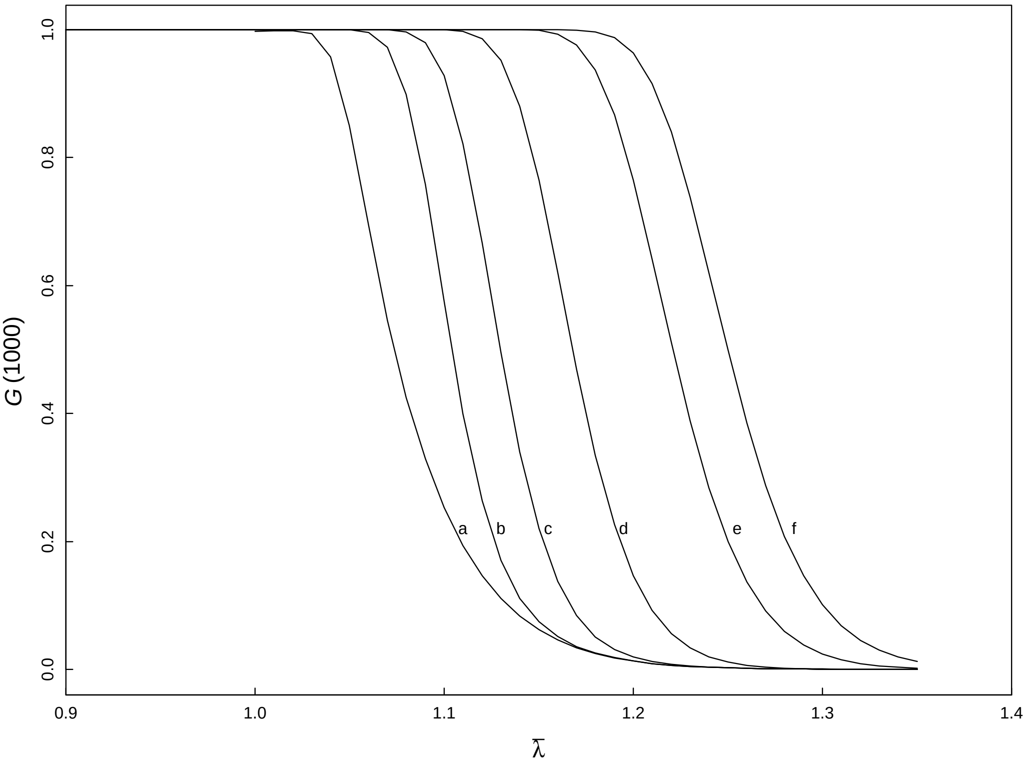


Figure 4.2. The probability of reaching the lower threshold by time T = 1000 for the linear model with an upper limit to population size [4.1] as the mean multiplicative growth rate, $\bar{\lambda}$, is increased. (a) no upper limit, (b) N_b = 100000, (c) N_b = 40000, (d) N_b = 20000, (e) N_b = 12000, (f) N_b = 10000. In all cases Var(λ) = 0.1, N_a = 3000, N_0 = 8000.

probability, $G(T) = \int_0^T g(t)dt$, of reaching the threshold by some time, T, which is large but finite.

Fig. 4.2 demonstrates that for times which are finite, but nevertheless long in ecological terms, the probability of reaching the threshold by T may be less than one for both the unrestricted and restricted models. The shape of the curve of $G(T)$ against $\bar{\lambda}$ is similar to that of $G(\infty)$ against $\bar{\lambda}$ for the unrestricted model (Fig. 3.6): as $\bar{\lambda}$ is increased past a certain level the probability that the threshold is reached by time T decreases rapidly. Thus, for fixed N_a, N_b, N_0 and Var(λ), there is a range of values of $\bar{\lambda}$ for which reaching the threshold by time T = 1000 is certain, but as $\bar{\lambda}$ is increased there is a rapid transition to the situation where $G(1000)$ is small. As the upper limit, N_b, is set at successively lower population sizes the curves of Fig. 4.2 are shifted to the right, such that the range of population growth rates for which reaching the threshold by $T = 1000$ is certain is increased.

For the unrestricted model of chapter 3 where the population growth rate was high the chance that a realisation reached the lower threshold depended a great deal on the sequence of environments encountered in the first few time steps. If a poor run of growth rates, taking the population to the threshold, was not encountered then the population grew rapidly away from the threshold. Those realisations that did reach the threshold did so at short times. With a hard upper limit to population size realisations do not have the "escape" mechanism of growing to very large sizes. Populations at any finite upper limit retain some probability of decline to the lower threshold, though for large upper limits (or low variance in a high growth rate) this probability may be very small.

In particular when μ is large, the persistence time distribution for the linear model restricted by an upper limit can be considered as consisisting of two parts: the tail of the distribution which relates to the probability that a population encounters a run of poor environments causing it to leave the region of the upper limit and reach the lower threshold; and (for all cases where $N_0 < N_b$) an "initial condition" part associated with the possibility that the lower threshold may be reached before the upper limit is ever encountered. This latter effect is the same effect as a realisation of

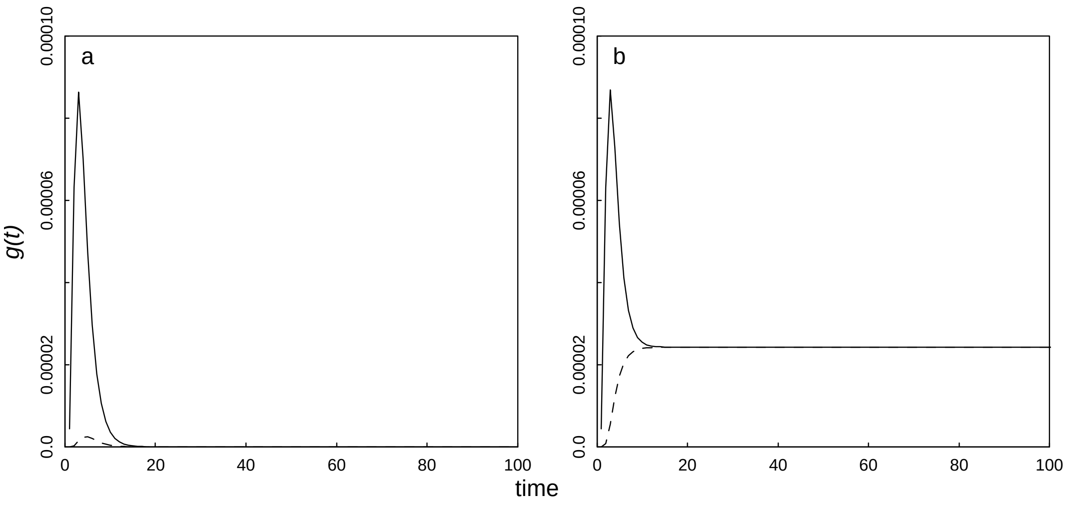


Figure 4.3. The persistence time distributions for $\bar{\lambda} = 1.3$, Var(λ) = 0.1 and $N_a = 3000$ with (a) no upper limit to population size, (b) an upper limit of 12000 individuals. —— $N_0 = 8000$, - - - - $N_0 = 12000$.

the unrestricted model encountering an initial run of low growth rates causing it to decline to the threshold size despite an overall high growth rate.

Fig. 4.3 demonstrates these effects. The persistence time distributions in Fig. 4.3a are for the unrestricted model, and those in Fig. 4.3b for the restricted model. The solid line shows the case where, for the restricted model, $N_0 < N_\mathrm{b}$. For t small the persistence time distributions for the two models are similar, the sharp peak corresponding to the few realisations that rapidly decline from the initial population size to reach the threshold. In the unrestricted model, after this initial peak, the probability of reaching the threshold is zero as the high growth rate causes populations to grow to infinite size. In the restricted model the tail of the distribution is raised, and declines only very slowly, representing the probability of leaving the region of the upper limit and reaching the lower threshold. If, in the restricted model, $N_0 = N_b$ (as shown by the dashed line in Fig. 4.3b) the initial peak disappears such that the persistence time distribution consists solely of the slowly declining tail.

Fig. 4.4 investigates the effect on mean and modal persistence time of changes in $\bar{\lambda}$ for the model with and without an upper limit to population size. The most striking differences are between the conditional means for the two models. As discussed in the previous chapter the conditional mean persistence time for the model with no upper limit declines rapidly from the point at which the long run growth rate becomes positive and ultimately reaching the lower threshold is no longer certain (marked by the vertical line in Fig. 4.4).

For the model with an upper limit, however, the conditional mean behaves rather differently. For lower values of $\bar{\lambda}$ the mean is similar to the model without upper limit. This is due to the fact that the long run growth rate is negative in both cases and all realisations decline rapidly to the lower threshold. When the long run growth rate is only slightly negative the mean persistence time in the model without the upper limit is characterised by high values resulting from the fact that some realisations have excursions to very high populations. Such excursions are prevented by the upper limit in the alternative model and the increase in mean persistence time is, therefore, not so dramatic. While the conditional mean in the unrestricted model declines sharply as soon as the long run growth rate becomes positive (and ultimately reaching the lower threshold is no longer certain), in the restricted model the mean persistence time continues to rise. This is because the upper limit prevents the

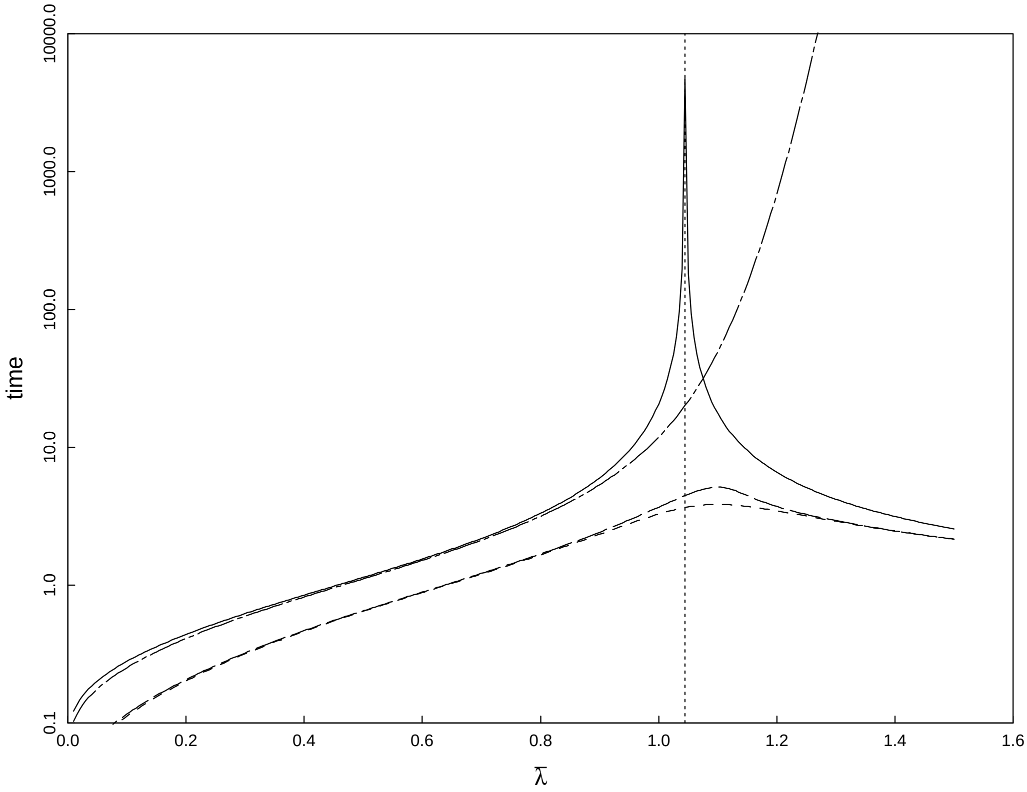


Figure 4.4. The conditional mean and modal persistence time for the simple multiplicative model with and without a limit to population size. Var(λ) = 0.1, N_0 = 8000, N_a = 3000, N_b = 12000. —— mean persistence time for model without upper limit, conditional on reaching the threshold (from eqn. [3.10]), — - — mean persistence time for model with upper limit (from eqn. [4.7]), – – – modal persistence time for model without upper limit (from eqn. [3.11]), — — — modal persistence time with upper limit (calculated numerically by Brent's method of function maximisation, Press *et al.* 1989). The dashed vertical line marks the value of $\bar{\lambda}$ at which the probability of ultimately reaching the lower threshold becomes less than one for the model with no upper limit.

growth of realisations to very large population sizes and the occasional realisation encounters a run of growth rates that enable it to leave the upper limit and reach the lower threshold. Thus, while the only realisations that reach the threshold in the unrestricted model are those that encounter a particularly "bad" run of growth rates early in the realisation, in the restricted model there remains a small probability of reaching the threshold even at quite long times. This results in the increase in the conditional mean persistence time seen in Fig. 4.4.

While the differences in conditional mean between the models with and without an upper barrier are striking, Fig 4.4 demonstrates that there are also differences between the model persistence times of the two models. As noted in the previous chapter, the peak in modal passage time for the unrestricted model occurs at a slightly higher value of $\bar{\lambda}$ than the peak in expected passage time. The modal passage time for the restricted model follows the same pattern, and for both low and high values of $\bar{\lambda}$ the modes are in fact the same. At intermediate values ($0.7 < \bar{\lambda} < 1.3$ for the parameters of Fig 4.4), however, the curves separate somewhat and the restricted model actually has slightly higher modal persistence times. For at least part of this range $G(\infty) = 1$ for the unrestricted, as well as the restricted, model so comparison is not complicated by different ultimate probabilities of reaching the lower threshold.

Fig 4.5 examines part of the persistence time probability density function for the restricted and unrestricted models with parameters which result in $G(\infty) = 1$ for both, but give a slightly longer modal passage time for the restricted model. The reason for

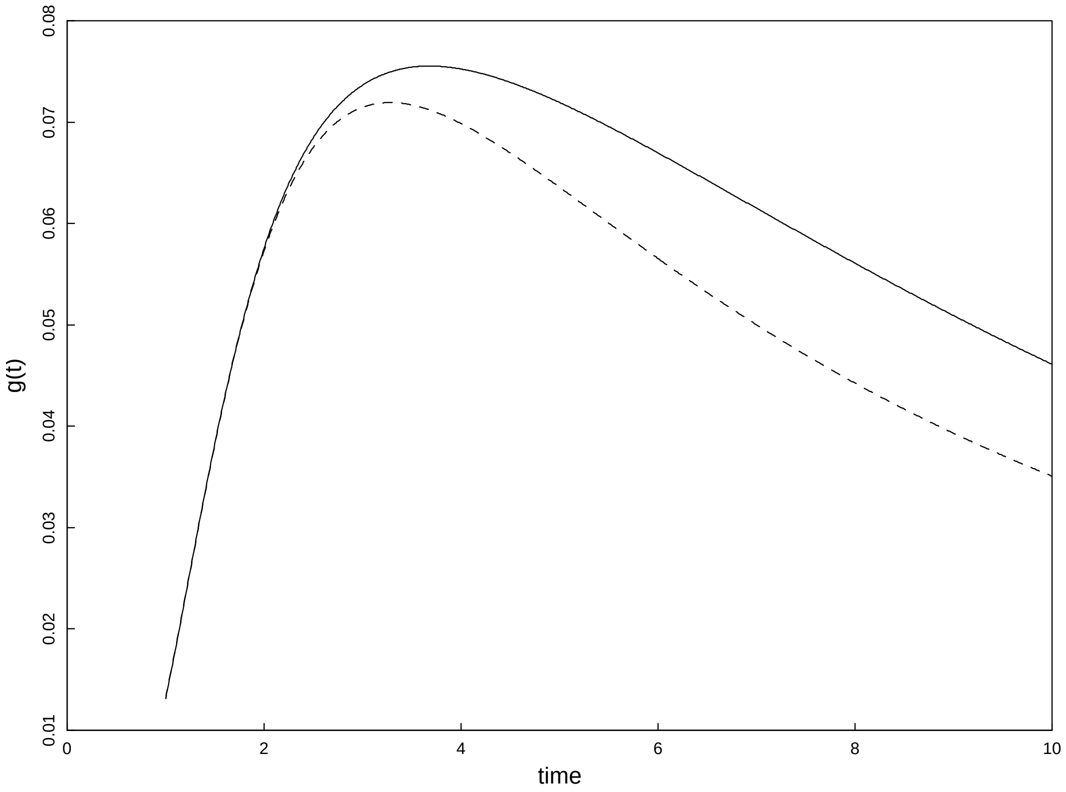


Figure 4.5. The persistence time probability density function for the unrestricted (– –) and restricted (——) ($N_b = 12000$) models. $\bar{\lambda} = 1$, $\mathrm{Var}(\lambda) = 0.1$, $N_0 = 8000$ and $N_a = 3000$.

the increase in modal persistence time for the restricted model is clear: for the part of the distribution illustrated, the distribution of persistence times for the restricted model has a raised tail relative to the unrestricted model, and this simply shifts the mode slightly to the right.

The increase in modal persistence time observed by restricting the population to sizes less than some upper limit is rather small, certainly not enough to suggest that the longevity of the population is enhanced in any way by the imposition of the barrier (this fact is obvious from Fig 4.5). Another way to look at this is to consider the probability of reaching the lower threshold before some time *t* (Fig 4.6). This confirms that, despite the slightly increased modal persistence time, the model with the upper barrier still represents a less favourable situation for the population as the probability of reaching the lower threshold is generally higher for the restricted model. The difference is greatest at intermediate times. Fig 4.6 also examines the effect of different upper limits on the probability of reaching the threshold by a

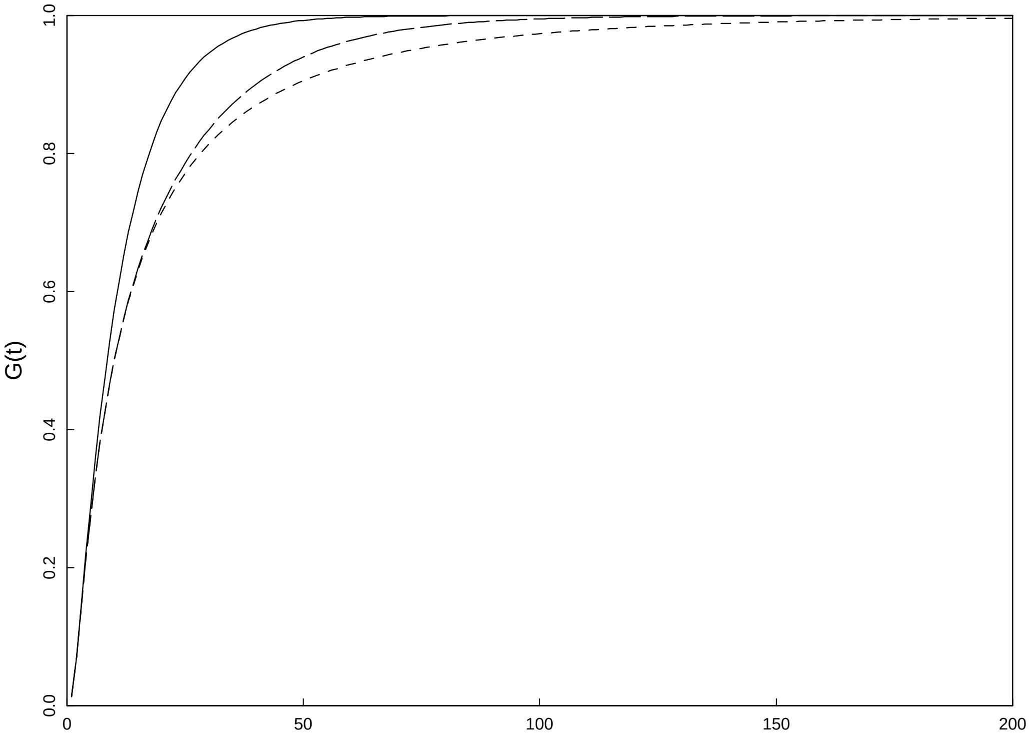


Figure 4.6. The probability of reaching the lower threshold by time *t* for the unrestricted (– –) and restricted (—— N_b = 12000, — — N_b = 30000) models. $\overline{\lambda}$ = 1, Var(λ) = 0.1, N_0 = 8000 and N_a = 3000.

certain time. Increasing the upper limit from 12000 to 30000 individuals greatly reduces the difference between the curves for the restricted and unrestricted models.

Fig. 4.7 examines the change in expected persistence time as the upper limit to population size is increased for a set of parameters which mean that ultimately reaching the lower threshold is certain. As the level of the upper limit is increased from a level not far above the initial population size the expected persistence time increases rapidly. However as the upper limit is increased further the increase in persistence time slows and appears to asymptote at the expected persistence time for the unrestricted multiplicative model. For cases where ultimately reaching the lower threshold is not certain the expected persistence time for the restricted model continues to rise, as a small probability of reaching the threshold persists for quite long times (Fig. 4.3). However, the modal persistence time for the restricted and unrestricted models is very similar in all cases (whether or not ultimately reaching the

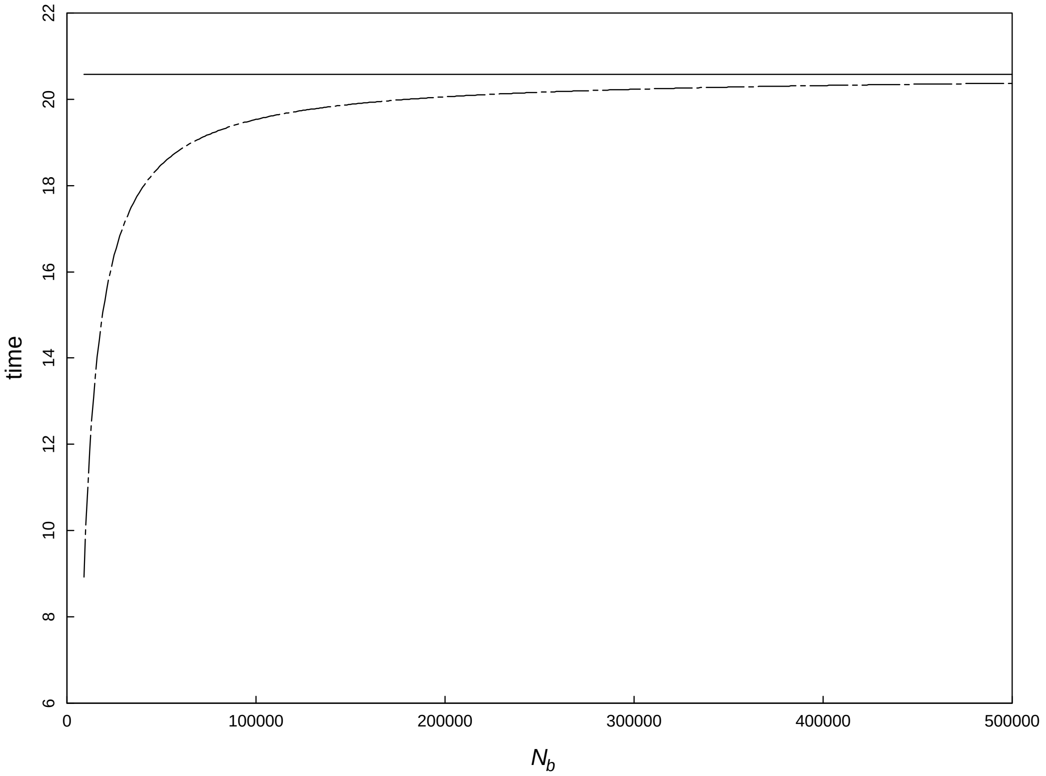


Figure 4.7. The mean persistence time for the restricted multiplicative model (— - —) as the upper limit to population size, N_b, is varied. —— mean persistence time for model without upper limit. $\overline{\lambda}$ = 1, Var(λ) = 0.1, N_0 = 8000, N_a = 3000.

lower threshold is certain).

Fig. 4.8 investigates the modal and mean persistence times in the unrestricted and restricted models as the variation of the multiplicative growth rate is increased. When the variation is such that ultimately reaching the lower threshold is certain in both the restricted and unrestricted models (all values to the right of the vertical line in Fig. 4.8) the effect of further increasing Var(λ) is essentially the same as that observed in Fig. 3.9, in that both mean and modal persistence times decrease. However, while the expected persistence time for the restricted model is less than the expected time for the unrestricted model (as excursions to large population sizes are

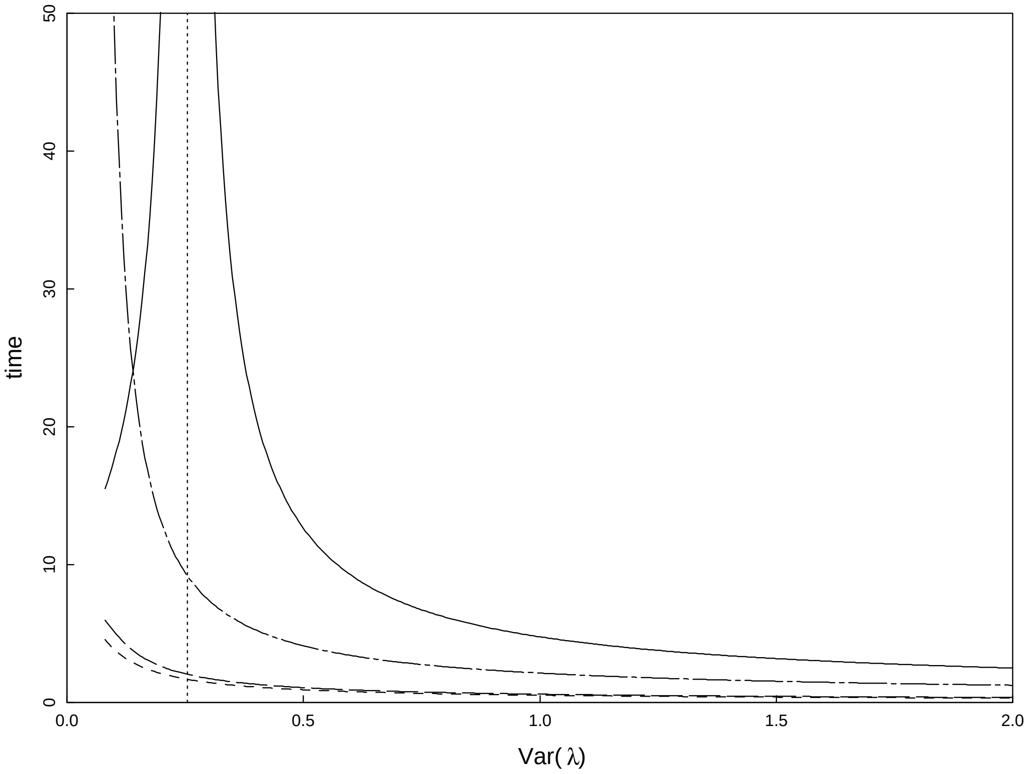


Figure 4.8. The conditional mean and modal persistence time for the simple multiplicative model with and without a limit to population size as Var(λ) is increased. $\overline{\lambda}$ = 1.1, N_0 = 8000, N_a = 3000, N_b = 12000. —— mean persistence time for model without upper limit, conditional on reaching the threshold (from eqn. [3.10]), — - — mean persistence time for model with upper limit (from eqn. [4.7]), – – – modal persistence time for model without upper limit (from eqn. [3.11]), — — — modal persistence time with upper limit (calculated numerically by Brent's method of function maximisation, Press *et al.* 1989). The vertical dotted line marks the point at which $G(\infty)$ becomes equal to one in the unrestricted model.

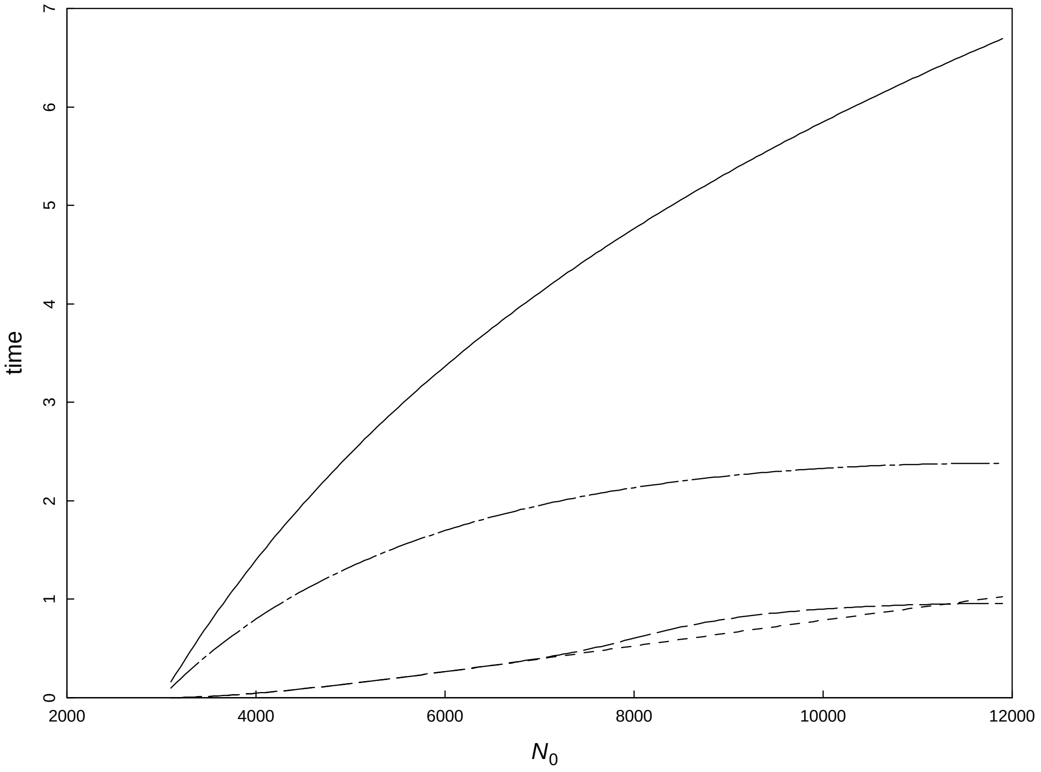


Figure 4.9. The conditional mean and modal persistence time for the simple multiplicative model with and without a limit to population size for different values of the initial population size, N_0. $\overline{\lambda}$ = 1.1, Var(λ) = 1, N_a = 3000, N_b = 12000. —— mean persistence time for model without upper limit (from eqn. [3.10]), — - — mean persistence time for model with upper limit (from eqn. [4.7]), – – – modal persistence time for model without upper limit (from eqn. [3.11]), — — — modal persistence time with upper limit (calculated numerically by Brent's method of function maximisation, Press *et al.* 1989).

prevented by the upper limit), the modal persistence times are very similar.

Figs. 4.9 and 4.10 examine the mean and modal persistence times as the initial population size, N_0, and the level of the lower threshold, N_a, respectively are varied for parameters where ultimately reaching the lower threshold is guaranteed in the unrestricted model. The pattern of change is similar for the unrestricted and restricted models in both cases. Like Fig 4.8, the expected persistence time in the restricted model is less than that of the unrestricted model, but the modal persistence times are very similar.

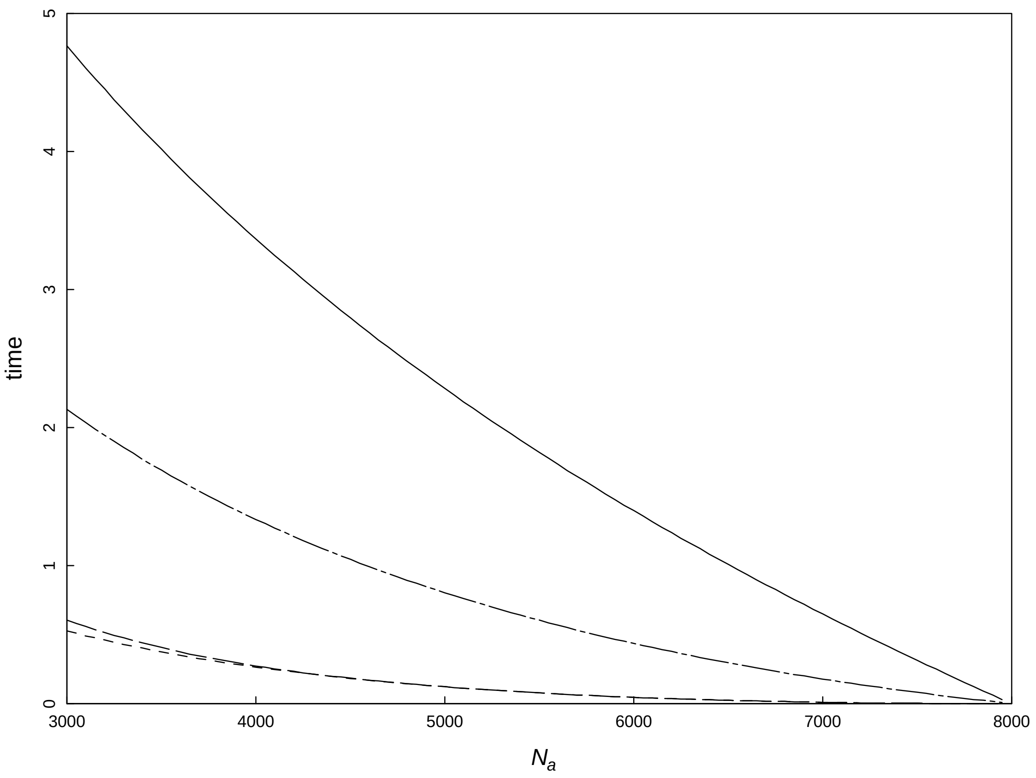


Figure 4.10. Change in the mean and modal persistence time for the simple multiplicative model with and without a limit to population size as the lower threshold, N_a, is increased. $\overline{\lambda} = 1.1$, $\mathrm{Var}(\lambda) = 1$, $N_0 = 8000$, $N_b = 12000$. —— mean persistence time for model without upper limit (from eqn. [3.10]), — - — mean persistence time for model with upper limit (from eqn. [4.7]), – – – modal persistence time for model without upper limit (from eqn. [3.11]), — — — modal persistence time with upper limit (calculated numerically by Brent's method of function maximisation, Press *et al.* 1989).

Discussion

Imposing an upper limit to population size on the simple linear model affects persistence time in various ways. Perhaps the most interesting effects are those which occur when the long run population growth rate is around zero. Here, the most marked feature of the unrestricted model of the previous chapter was the fact that very long expected persistence times could arise even when the ultimately reaching the lower threshold was certain. Indeed where the long run growth rate was equal to zero the unrestricted model had an infinite mean persistence time. In the restricted model the mean persistence time is finite for $\mu = 0$. While the imposition of an upper limit to population size reduces the expected persistence time in such situations (Fig.

4.4), this results mainly from the fact that populations are prevented from growing to infinite size. In contrast with the mean persistence time, the modal persistence time is generally not reduced by the presence of the upper barrier, even when the upper limit is set at a fairly small number of individuals (Figs. 4.4, 4.5).

For cases where the ultimate probability of reaching the lower threshold is comparable, the pattern of variation in the mean and modal persistence times tends to be similar in the restricted and unrestricted models. In general, the expected persistence time is rather less in the model with an upper limit, but the modal persistence times are virtually the same. Thus the major effect of an upper limit to population size is to eliminate population fluctuations to large sizes. This appears to have rather little effect on the most likely persistence time.

In one respect all that the upper limit to population size actually does is make the linear model more realistic, as no environment could support an infinitely large population. However, from the point of view of population management it is of some reassurance that in some cases a reductions in the number of individuals that a habitat can support does not greatly affect the most likely persistence time of the population.

At the end of the previous chapter it was suggested that the argument, from random walk models, that persistence of a population required density dependent regulation of population size should really be abandoned. This was suggested for two reasons: the fact that there was a finite probability of not reaching a lower threshold if the long run growth rate was positive, and the fact that, even when reaching the threshold was certain, some populations may still persist, unregulated, for very long times. One criticism that could be made of this argument is that the linear model allowed the (unrealistic) possibility of infinitely large populations. This possibility is excluded by the imposition of an upper barrier. While reaching the lower threshold is ultimately certain in the restricted model considered in this chapter, as Fig. 4.2 shows, there are occasions where the probability of reaching the lower threshold by some long time, T, is small.

In general then, the linear model with an upper limit to population size is similar to the linear model of chapter 3 which had no upper limit. The main effect of the upper limit is to eliminate the unrealistic infinite population sizes that could arise in the unrestricted linear model.

An example: the Acorn woodpecker in New Mexico

Stacey & Taper (1992) present a simulation model to investigate persistence in the acorn woodpecker, *Melanerpes formicivorus,* which occurs in small, rather isolated, populations in the southwest of the United States. They present data relating to the population of woodpeckers in a single canyon in the Magdalena Mountains of New Mexico from 1975 to 1984. The population is thought never to be greater than 60 individuals and a large proportion are colour ringed allowing calculation of survivorship and reproductive rates from individual histories. Stacey and Taper's data is reproduced in Table 4.2.

Stacey & Taper construct a simulation model to investigate the likely persistence time of the population in the absence of interchange with other breeding groups, and assuming that the calculated demographic parameters are density independent. From the description given it is possible to write the model in the form of a difference equation:

$$N_{t+1} = \begin{cases} r_t \frac{N_t}{2} j_t + a_t N_t & \text{if } \left[r_t \frac{N_t}{2} j_t + a_t N_t \right] \leq N_b \\ N_b & \text{otherwise} \end{cases} \qquad [4.8]$$

where N_t is the population size at the start of the breeding season in year t, r_t is the reproductive rate per pair, j_t is the probability that a fledgling survives to breed in year $t + 1$, and a_t is the probability that an adult survives to breed in the subsequent year. I have represented Stacey & Taper's "carrying capacity" by N_b. This is the maximum number of breeding individuals that the area can support, twice the maximum number of breeding pairs. The number of territories for the acorn woodpecker appears to be determined by the availability of acorns and other nuts which are collected by the birds in autumn and stored in holes in "granary trees" as a winter food supply (Stacey 1979). In their model Stacey & Taper assume that any excess of birds over the maximum number determined by the limited number of territories available are lost to the system. This imposes a reflecting boundary, referred to in this chapter as an upper limit to population size, at N_b. The population is considered to be extinct if it falls below two breeding individuals in size. Stacey & Taper assess persistence time using simulation where the yearly demographic parameters are drawn, independently, from the sets of observed values. However the analytic results presented in this chapter may easily be applied to give analytic results for the model with no immigration.

In the absence of the upper limit, the model [4.8] can be written in the form of the general multiplicative model

$$N_{t+1} = \lambda_t N_t \qquad [4.9]$$

where

$$\lambda_t = \frac{r_t j_t}{2} + a_t \qquad [4.10]$$

Applying this to the data of Table 4.2 yields a mean multiplicative growth rate of 0.987 with a (sample) variance of 0.114. Inserting these values in equations [3.6]

Table 4.2. Stacey & Taper's (1992, Table 1) data for the population of acorn woodpeckers in Water Canyon, New Mexico. Population size is the total number of birds residing in the study area in May at the start of the breeding season. Adult survivorship represents the probability that an individual alive at the start of the year's breeding season would still be alive at the start of the next year, while juvenile survivorship represents the probability that a bird survives from fledging to the start of the following breeding season. Survivorships were calculated from the histories of ringed individuals. Annual reproductive success is the mean number of young produced per breeding pair, from observations of all nesting attempts. Birds known to have survived the winter but which left the area before the breeding season are recorded as emigrants.

Year	Adult survivorship	Juvenile survivorship	Reproductive rate (young/pair)	Population size (no. adults)	Number of emigrants
1975	0.53	0.56	3.38	46	3
1976	0.68	0.64	1.27	46	4
1977	0.71	0.30	2.77	40	1
1978	0.38	0.40	2.17	51	2
1979	0.54	0.00	0.05	52	0
1980	0.69	0.38	4.00	32	0
1981	0.66	0.18	2.37	46	1
1982	0.49	0.25	0.50	49	1
1983	0.61	0.44	1.60	35	1
1984			2.00	36	
mean	0.588	0.350	2.011	43.3	1.44
sample variance	0.012	0.038	1.490	50.01	1.78

gives the long run population growth rate, μ, as –0.069 and the infinitesimal variance, σ^2, as 0.111. These values can be used in conjunction with [4.3] to provide the probability density of persistence times in the closed population model. The distribution of persistence times predicted by [4.3] is shown in Fig. 4.11 (solid line) with a histogram, reproduced from Stacey & Taper's Fig. 2, showing the results of a "typical run" of their simulation model for a closed population. It is immediately apparent that the two do not agree very closely.

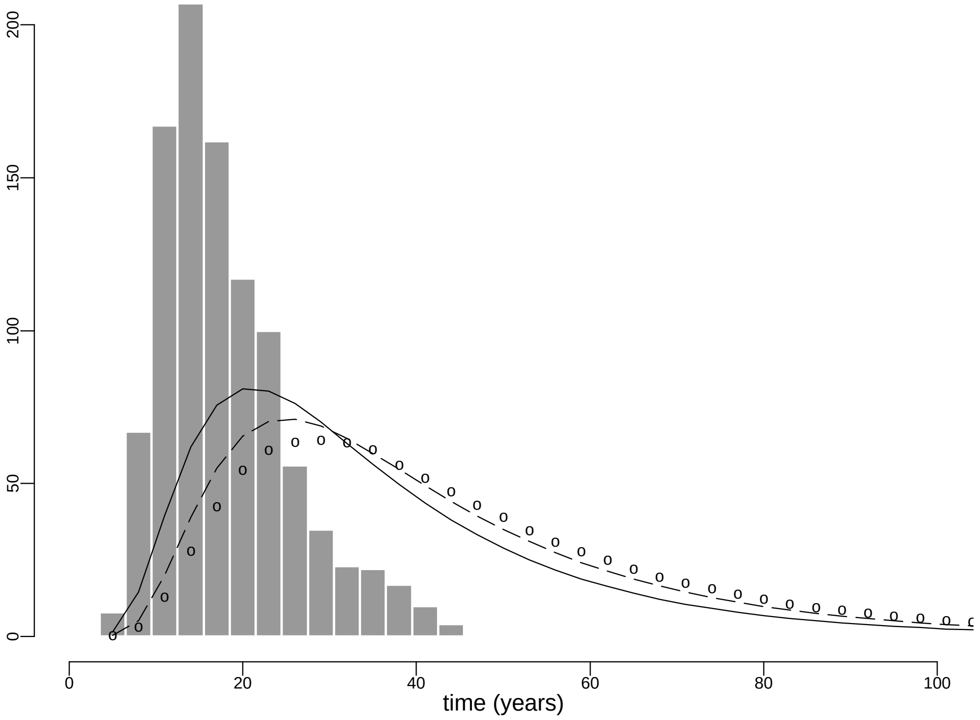


Figure 4.11. Stacey & Taper's (1992, Fig. 2) persistence time distribution for a closed population (histogram) compared with the persistence time distributions obtained from [4.3] with (solid line) parameters assuming observed values are samples drawn from some distribution, and (broken line) parameters from mean and variance of the 720 λ values that can arise using Stacey & Taper's simulation method. Open circles represent numerical estimate of persistence time distribution of [4.8] using values drawn at random from Table 4.2 and excluding the 1979 juvenile survival value. In order to produce persistence time distributions comparable with Stacey & Taper's Fig. 2 the probability of reaching the lower threshold has been integrated over three year intervals and multiplied by 1000 (the number of simulations that went into Stacey & Taper's persistence time histogram). N_h = 52 individuals.

In an effort to uncover the reason for the discrepancy between the two, I implemented Stacey & Taper's simulation model exactly as they described, calculating the change in population size each iteration of the model [4.8] by randomly selecting one of the observed values for reproductive rate per pair, juvenile and adult survival (excluding the 1979 zero value for juvenile survival). The results of this exercise are shown as the open circles on Fig. 4.11, again very different from Stacey & Taper's result.

Before considering the reason for the discrepancy between Stacey & Taper's simulated persistence time distribution and the analytical and numerical persistence times calculated here, it is first of interest to consider the less marked discrepancy between the analytical persistence time distribution (the solid line in Fig. 4.11) and the numerical distribution marked by the open circles on Fig 4.12. This discrepancy is largely due to the simulation methodology employed. In the analytical treatment above, the data of Table 4.2 for which reproductive rate, juvenile survival and adult survival were known (i.e. 1975 to 1983) were used to calculate a long term rate population growth rate, μ, and its variance, σ^2, and these values were used to produce the persistence time distribution using [4.3]. In the simulated persistence time distribution the value for juvenile survival for 1979 is excluded and the reproductive rate for 1984 is included. Perhaps most important, however, is the fact that the values of Table 4.2 represent the complete set of rates incorporated in the simulation and the sample variance of λ, used to calculated the variance in the long run growth rate will therefore overestimate the realised variance. If the mean and variance of the 720 possible combinations of r_t, j_t and a_t actually used in the simulation are used to calculate the persistence time distribution the broken line in Fig. 4.11 results, which is rather closer to the simulated distribution. This illustrates the problem of Stacey & Taper's methodology in considering the set of observed values for the demographic parameters to be the only possible values, rather than samples from some distribution.

Returning to the problem of the rather larger discrepancy between Stacey & Taper's simulated persistence time distribution for the closed population and the distribution obtained here, it seems, initially, that a rather simple explanation may be forthcoming. While Stacey & Taper's explanation of their simulation model makes no mention of emigration, it would appear that their simulation model for the closed population does in fact involve subtracting one of the observed emigration values such that [4.8] should, in fact, read

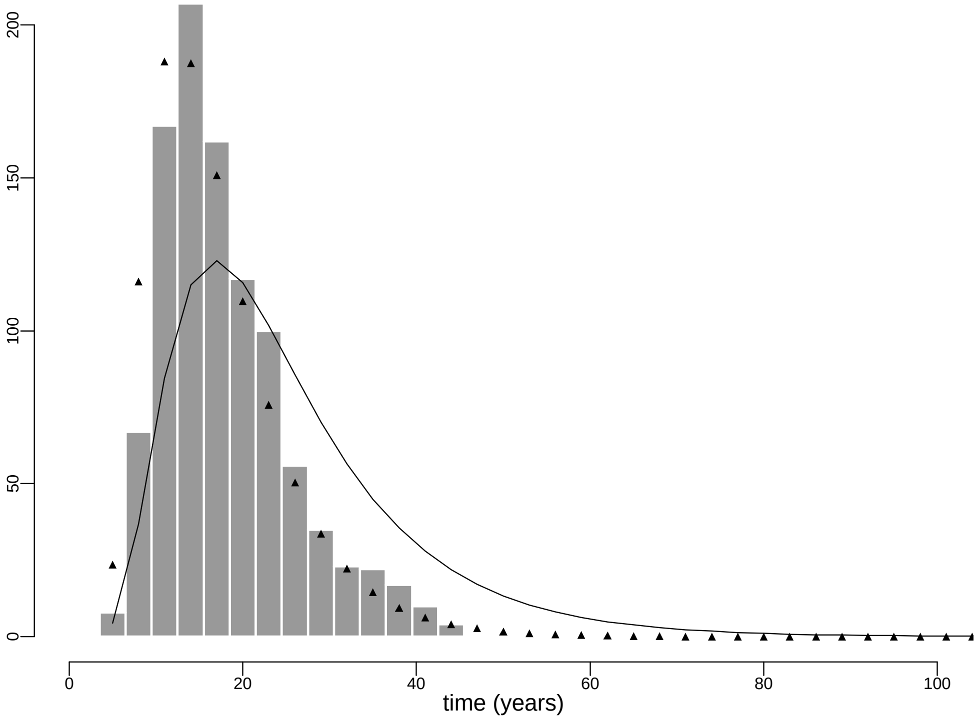


Figure 4.12. Simulated persistence time distribution (triangles) from [4.11] where r_t, j_t, a_t, and E_t are chosen at random from the values of Table 4.2 (excluding the 1979 juvenile survival value), compared with Stacey & Taper's (1992, Fig. 2) persistence time distribution for a "closed population" (histogram). The solid line is given by the formula [4.3] when emigration is included as a component of adult survival (see text).

$$N_{t+1} = \begin{cases} r_t \dfrac{N_t}{2} j_t + a_t N_t - E_t & \text{if } \left[r_t \dfrac{N_t}{2} j_t + a_t N_t - E_t \right] \le N_b \\ N_b & \text{otherwise} \end{cases} \qquad [4.11]$$

where E_t is the number of individuals lost through emigration. Allowing for emigration by randomly selecting one of the observed numbers of emigrating individuals each iteration of the model produces a numerical persistence time distribution very close to that presented by Stacey & Taper (Fig. 4.12).

Stacey & Taper's aim in modelling the acorn woodpecker population as if it were closed is to provide a baseline against which to measure the importance of additional factors (immigration and density dependence) in ensuring population persistence. It is debatable whether the assumption that the population is closed should force individuals known to have emigrated from the population (despite the fact it was below the maximum of 52 individuals) to remain in the population, or whether these should be treated as additional losses. Despite their explanation, Stacey & Taper seem to have chosen to treat these as additional losses. Thus, to adequately apply the theory developed in this chapter, the mean and variance of the multiplicative growth rate, λ_t, must be calculated treating the individuals known to have emigrated as deaths. Defining α_t to be the compound survivorship representing the probability that a breeding adult in year t has not died or emigrated by the beginning of the breeding season in year $t + 1$ leads to the expression

$$\alpha_t N_t = a_t N_t - E_t \qquad [4.12]$$

Using α_t instead of a_t in the calculation of the multiplicative growth rate gives an expression for the multiplicative growth rate in each of the years for which data is available

$$\lambda_t = \frac{r_t j_t}{2} + \frac{a_t N_t - E_t}{N_t} \qquad [4.13]$$

which leads to a mean of 0.955 and a variance of 0.109 (see Table 4.3). This is equivalent to a long run growth rate (μ) of –0.103 with variance 0.113. These values, when inserted in [4.3], result in the persistence time distribution given by the solid line in Fig. 4.12. Despite the incorporation of emigration in the estimated multiplicative growth rate, the persistence time distribution that results from Stacey & Taper's simulation method is still not well represented by the simple multiplicative model with an upper limit. Stacey & Taper's simulations predict smaller modal persistence times and have a considerably shorter tail of long persistence times than the model distribution.

The reason for the continuing discrepancy between the model of this chapter and the simulations carried out by Stacey & Taper seems to be due to their simulation methodology. While they checked that the adult and juvenile survival rates, and the reproductive rate, were not correlated with each other they do not appear to have considered correlations between these parameters and the number of individuals emigrating each year, despite the fact that the observed emigration values have apparently been included in the simulation. In fact there is a significant positive correlation between the observed juvenile survival rate and the number of individuals surviving the winter, but leaving the population prior to breeding (Spearman's rank correlation, ρ = 0.7625, p = 0.0165 [one sided test]). The effect of neglecting this correlation and treating the emigration rate as an independent parameter, as Stacey &

Taper appear to have done in their simulations, is to subtly introduce inverse density dependence. There are 6480 combinations of the observed survival, reproductive and emigration rates, excluding the 1979 juvenile survival rate. Using [4.13] the mean multiplicative growth rate, where a_t, j_t, r_t and E_t are chosen independently from the set of observed values, can be calculated for all population sizes between the lower bound of two individuals and the upper bound of 52 individuals, as determined by the number of available territories. This is illustrated in Fig. 4.13, which demonstrates that the mean growth rate declines dramatically when the population size falls below 10 to 15 individuals.

A similar situation results if the survival and reproductive rates are chosen from normal distributions and the number of emigrants from a poisson distribution. This

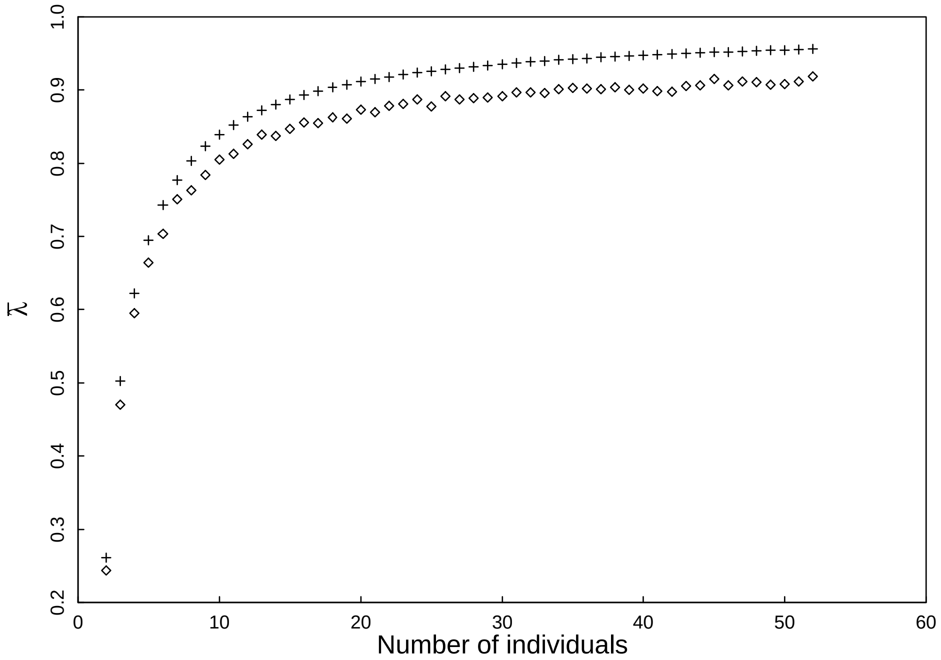


Figure 4.13. The spurious inverse density dependence introduced into the multiplicative growth rate as a result of choosing emigration rate independently from the observed data (+). The mean growth rate, $\overline{\lambda}$, was calculated by taking the mean of the 6480 possible combinations of demographic parameters at each population size and applying eqn. [4.13]. A more general model where a_t, j_t and r_t are chosen from normal distributions with mean and variance from the data of Table 4.2, and E_t from a poisson distribution with mean from the data of Table 4.2 produces a similar result - each point (◊) is the mean of 8000 values of lambda where the component demographic parameters have been chosen independently.

is due to the fact that at smaller population sizes a given number of emigrants represent a larger proportion of the population than they would do at larger population sizes. Stacey & Taper thus fail in their stated aim of establishing the likely persistence time for a closed population with a density independent growth rate.

This spurious fall in growth rate at smaller population sizes is responsible for the shorter persistence times observed in Stacey & Taper's simulations relative to the persistence times predicted by the model of this chapter. Because the method of estimating the multiplicative growth rate employed here [4.13] does not rely on the independence of any of the demographic components, the solid line in Fig. 4.12 is likely to be a better indication of the distribution of persistence times for the acorn woodpecker population in the absence of immigration. However, despite the problems with Stacey & Taper's simulation method noted here, many of their conclusions are supported by the application of the methods of this chapter. For the case where the population growth rate is estimated with the inclusion of the observed emigration the modal persistence time is seventeen years (this increases to 21 years for the model [4.8] where the population is truly closed and emigration is prevented). The probability of persistence for 70 years in the model where emigration is permitted is less than 0.01. While this is considerably larger than the probability of < 0.000001 that Stacey & Taper estimate from their simulations, it still suggests that survival for this length of time is relatively unlikely (given that the mean and variance of the multiplicative growth rate do not change). As Stacey & Taper report, the population of acorn woodpeckers in Water Canyon is known to have survived for at least 70 years. They consider two candidate mechanisms that may lead to increased persistence times: immigration from other subpopulations in the Magdalena Mountains, and density dependence leading to an increased population growth rate at low numbers.

The effects of immigration on persistence time can be incorporated in the model by a similar mechanism to that used to incorporate emigration. If the population growth rate for each of the years 1975 to 1983 is recalculated using the formula

$$\lambda_t = \frac{r_t j_t}{2} + \frac{a_t N_t - E_t + I}{N_t} \qquad [4.14]$$

where I is the effective immigration rate (that is, the number of individuals arriving in Water Canyon and successfully joining the breeding population each year) then it

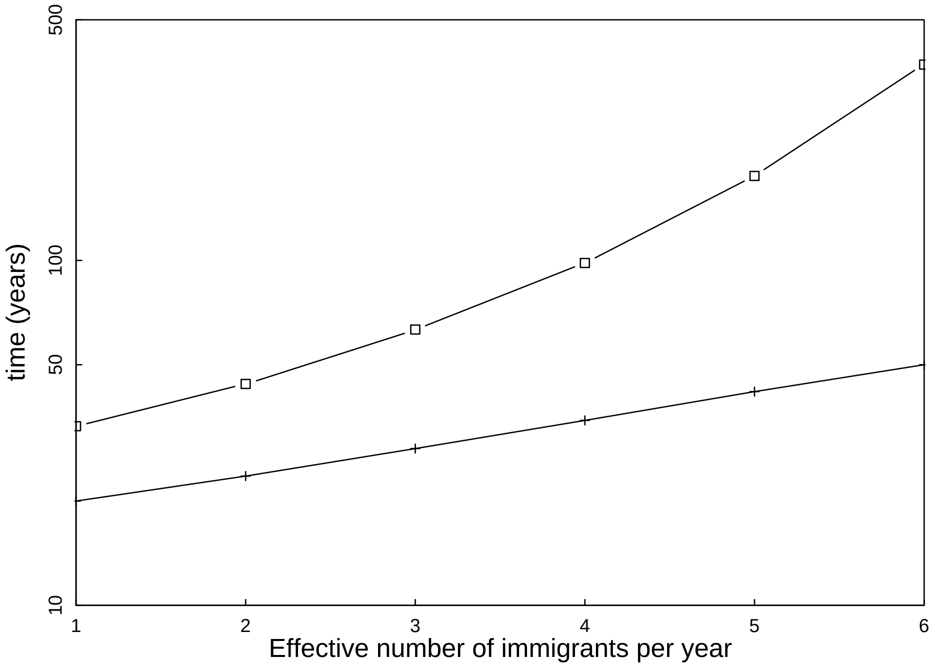


Figure 4.14. The effects on mean (•) and modal (+) persistence time of a set number, *I*, of individuals joining the population each year. Note that the ordinate is plotted on a logarithmic scale.

is possible to again estimate the mean and variance of this multiplicative growth rate for different levels of effective immigration. The effects on persistence time are demonstrated in Fig. 4.14. In common with Stacey & Taper's results persistence time increases substantially as the effective number of immigrants per year is increased.

In fact, there is considerable evidence from the data of Table 4.2 that interchange with other breeding groups is an important factor in the Water Canyon woodpecker population dynamics. The number of immigrants each year can be inferred by calculating, using [4.11], the size of breeding population that would be expected in the absence of immigration and relating this to the actual breeding population recorded (Table 4.3).

In most years there is evidence for an effective immigration of up to around 10 individuals. In two years (1977, 1977), however, a negative number of immigrants is produced by this method. In the analysis above it was assumed that excess birds over the maximum number of breeding individuals that the canyon could support were lost to the population. In fact emigration to other subpopulations may be occurring at

Table 4.3. Various quantities derived from the data of Table 4.2. The multiplicative growth rate, λ_t, without emigration is given by [4.10]; the expected number of adults is the number of adults predicted each year from the observed demographic rates without any emigration or immigration (from [4.8]), and the estimated immigration is the difference between the expected number of breeding adults and the observed number, taking account of known emigrants. The compound survival is given by [4.12] and the multiplicative growth rate, λ_t, with emigration is by [4.13].

Year	λ_t without emigration	Expected no. of adults	Estimated immigration	Compound survival, α_t	λ_t with emigration
1975	1.48			0.46	1.41
1976	1.09	67.91	-17.91	0.59	1.00
1977	1.13	49.97	-8.97	0.69	1.10
1978	0.81	45.02	7.98	0.34	0.77
1979	0.54	41.51	10.49	0.54	0.54
1980	1.45	28.08	3.92	0.69	1.45
1981	0.87	46.40	0.60	0.64	0.85
1982	0.55	40.17	9.83	0.47	0.53
1983	0.96	27.07	8.93	0.58	0.93
1984		33.67	2.33		
mean	0.987			0.556	0.955
sample variance	0.114			0.013	0.109

levels greater than those recorded. This is closely related to the discussion at the end of chapter 3 where it was suggested that fragmented populations may persist longer than any of the sub-populations involved. In the case considered here, the upper limit to the number of breeding territories may produce a form of density dependent emigration. Assuming that the environmental variation, which seems to influence juvenile survivorship in particular, affects subpopulations independently to some extent then excess individuals from a good year's breeding in one subpopulation may swell the numbers of another subpopulation which experienced a poorer recruitment. Such interchange will, of course, not only produce longer persistence in the component subpopulations, but lead to persistence of the species in the wider area. As Stacey & Taper point out, the acorn woodpecker appears to have solved the problem of persistence in a fragmented resource landscape. Again, see Gilpin & Hanski (1991) for further consideration of the dynamics of fragmented populations.

The other mechanism postulated as contributing to persistence times greater than those predicted by the model of [4.11] was an increased population growth rate at small population sizes. As the plots of Fig. 4.15 show, there is ample evidence in Stacey & Taper's data (Table 4.2) that such density dependent effects do occur. While the survival rate of fledged young appears largely independent of population size, both adult survival and the mean number of young per pair show evidence of a decrease with increasing population size (though neither are quite significant at the 5% level when a simple linear regression is calculated). When known emigrants are included with adult survival to produce an estimate of compound survival, a significant decrease in survival with population size is observed. The assumed net interchange of birds with other acorn woodpecker subpopulations also shows a significant decrease with the predicted population size in the absence of interchange. This is heavily influenced by the three negative values representing emigration of significantly more individuals than actually observed. The ratio of the observed breeding population in one year to that in the preceding year measures the realised population growth rate. Again a significant decrease with increased population size is observed, suggesting that the actual "equilibrium" population size is around 44 individuals.

Stacey & Taper do incorporate the effects of density dependence in their simulation model. They fit various models to the growth rate defined, quite properly, as $r_t = \ln(N_{t+1} / N_t)$. Unfortunately their Fig. 5, which plots this growth rate against population size, shows growth rates which bear scant resemblance to the values that should occur given the data they present. For instance, their plot suggests that only one value of r_t is positive. The data of Table 4.2 suggest there should, in fact, be five positive values. As their simulations of density dependent models are based on fitting various models to the growth rates they show, their results should be treated with some caution. However their general conclusion, that persistence times are enhanced by density dependent effects acting to regulate the woodpecker population around some "equilibrium" size, seems sound.

Various analytical methods to determine the effect of density dependent growth rates on the persistence time of populations are investigated in subsequent chapters. However, the example provided by the acorn woodpecker demonstrates the usefulness of the simple multiplicative model with an upper limit to population size in the analysis of the persistence of real biological populations.

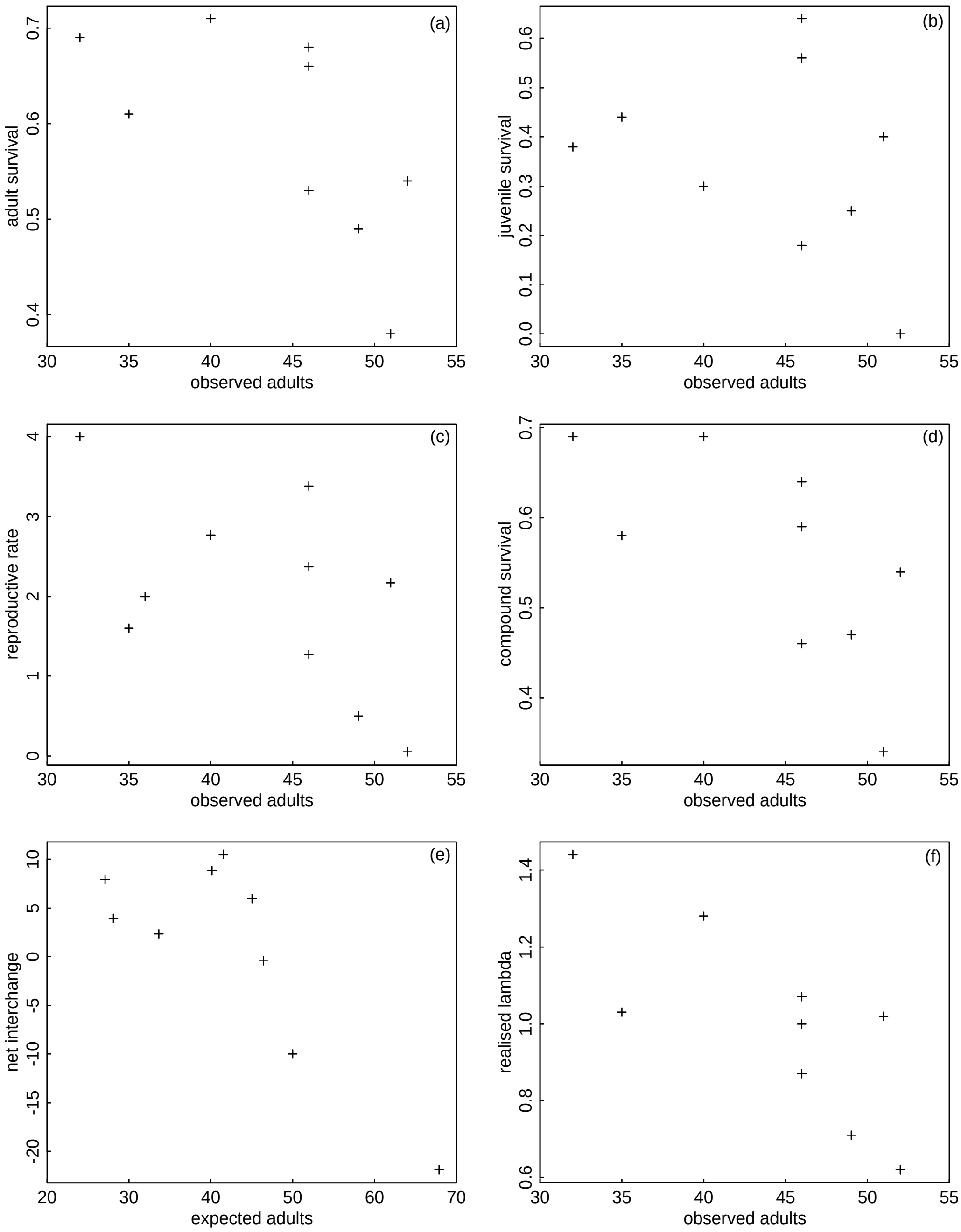
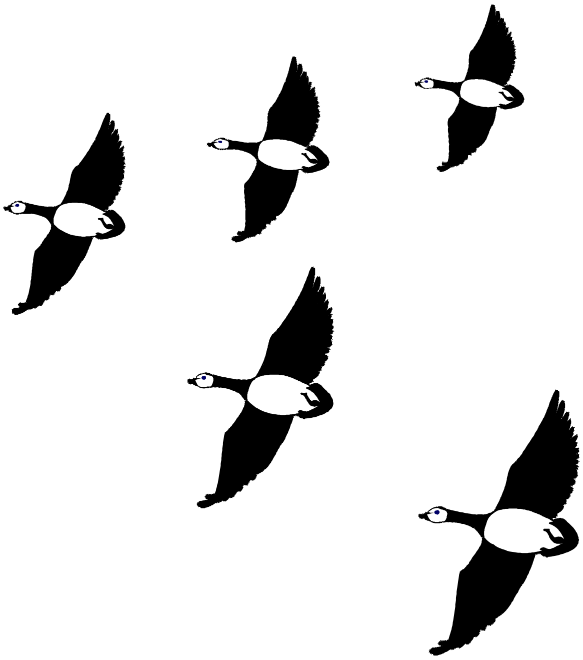


Figure 4.15. The relation of various demographic parameters to population size. Probability values given are the probability that slope resulting from a linear least squares regression is zero. (a) Measured adult survival against observed number of breeding adults (p = 0.0576); (b) juvenile survival versus breeding adults (p = 0.434); (c) reproductive rate versus breeding adults (p = 0.0944); (d) compound survival (from [4.12]) against breeding adults (p = 0.0464); (e) net assumed interchange (the difference between the number of observed breeding adults and the expected number of breeding adults from [4.8]) against the expected number of adults (p = 0.0088); (f) the realised population growth rate (N_{t+1}/N_t) against the observed number of breeding adults in year t (p = 0.0133).



Chapter 5

Persistence time in density dependent models

Introduction

Approximation of the persistence time distributions of the linear models discussed in chapters 3 and 4 by the first passage time distributions of the Wiener process with suitable boundary conditions provided a very general result for persistence time in density independent population models. In contrast, the wide variety of ways in which density dependence can be formulated means that such general results for non-linear models are unlikely to be forthcoming. In order to gain a feeling for the kind of persistence time distributions that may arise in density dependent models, this chapter examines persistence time in stochastic interpretations of the familiar logistic model which remains the most widely known density dependent population model, despite problems of assigning practical ecological meaning to its parameters.

Two distinct approaches to the problem of persistence in logistic models are investigated here: (i) transformations of the stochastic differential equation such that the first passage time results for the Wiener and Ornstein Uhlenbeck processes (chapter 2) can be invoked to provide exact results for the persistence time; and (ii) an examination of whether persistence time results for locally linear approximations to the full non-linear models can provide useful information on persistence time in the full model. While neither approach is without problems, some qualitative features of persistence time are forthcoming, at least for the case where a population is regulated around some mean value.

Exact results for continuous time stochastic logistic models

Despite its encouraging title this section reports work which is limited by some quite severe restrictions, both in the models employed and the methods used. The work here follows up work by Goel & Richter-Dyn (1974) using their methods to investigate persistence time in a logistic model. In contrast to the other models considered in this thesis which are phrased in discrete time (but use continuous time approximations) the starting point here is the continuous time logistic. In the well known deterministic logistic model the change in population size through time is described by the differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad [5.1]$$

A common approach to considering the effect of environmental variation in such deterministic models is to replace one of the constant parameters (*r* or *K*) by a randomly varying parameter with some mean and a variance term given by scaled white noise, giving rise to a stochastic differential equation. This "heuristic" approach (Turelli 1977) contrasts with the situation in chapter 2 where stochastic differential equations arose as continuous time limits of discrete models. The non-linear stochastic differential equations in this chapter have the general form

$$dX(t) = \alpha(x)dt + \beta(x)dW \qquad [5.2]$$

In contrast to the cases considered in chapter 2, β is now a function of x. This means that the problem, which was only alluded to previously, of different ways of interpreting such SDEs must now be tackled. These difficulties arise, as before, from the fact that white noise is not a smooth differentiable function.

Ito and Stratanovich calculi

The two most popular interpretations of stochastic differential equations, such as [5.2], are known as the Ito and Stratanovich calculi (Feldman & Roughgarden 1975; Turelli 1977). In the present context the most important difference between these two interpretations is that they provide different ways of relating the stochastic differential equation to the diffusion process

$$\frac{\partial}{\partial t} p\left(x,t\middle|x_0\right) = -\frac{\partial}{\partial x}\left[v(x)p\left(x,t\middle|x_0\right)\right] + \frac{\partial^2}{\partial x^2}\left[w(x)p\left(x,t\middle|x_0\right)\right] \qquad [5.3]$$

and it is by manipulation of the diffusion equation that results relating to the persistence time will be obtained. Under the Stratanovich interpretation of the stochastic differential equation, the infinitesimal mean and variance of the diffusion equation are given by (Turelli 1977, Roughgarden 1979, p.380-381):

$$\begin{aligned} v(x) &= \alpha(x) + \frac{1}{4}\frac{\partial}{\partial x}\beta^2(x) \\ w(x) &= \beta^2(x) \end{aligned} \qquad [5.4]$$

whereas the Ito interpretation gives

$$\begin{aligned} v(x) &= \alpha(x) \\ w(x) &= \beta^2(x) \end{aligned} \qquad [5.5]$$

The simplest way to *numerically* integrate a stochastic differential equation is to use Euler's method (Nisbet & Gurney 1982, p.275). This method, however, corresponds to an Ito interpretation of the SDE. One way round this difficulty is to apply the method suggested by Nisbet & Gurney (1982). They point out that it is possible to associate two different stochastic differential equations with a given, well defined, diffusion process by applying either [5.4] or [5.5]. The process is illustrated in Fig.

5.1. The starting point here is the stochastic differential equation heuristically derived from the deterministic model. By applying the Stratanovich interpretation [5.4] a well defined diffusion process is obtained. Then, by asking the question "what stochastic differential equation would have led to this diffusion equation had the Ito interpretation been used ?", a different stochastic differential equation is obtained. By numerically integrating the two stochastic differential equations using Euler's method, both Ito and Stratanovich interpretations of the original stochastic differential equation result.

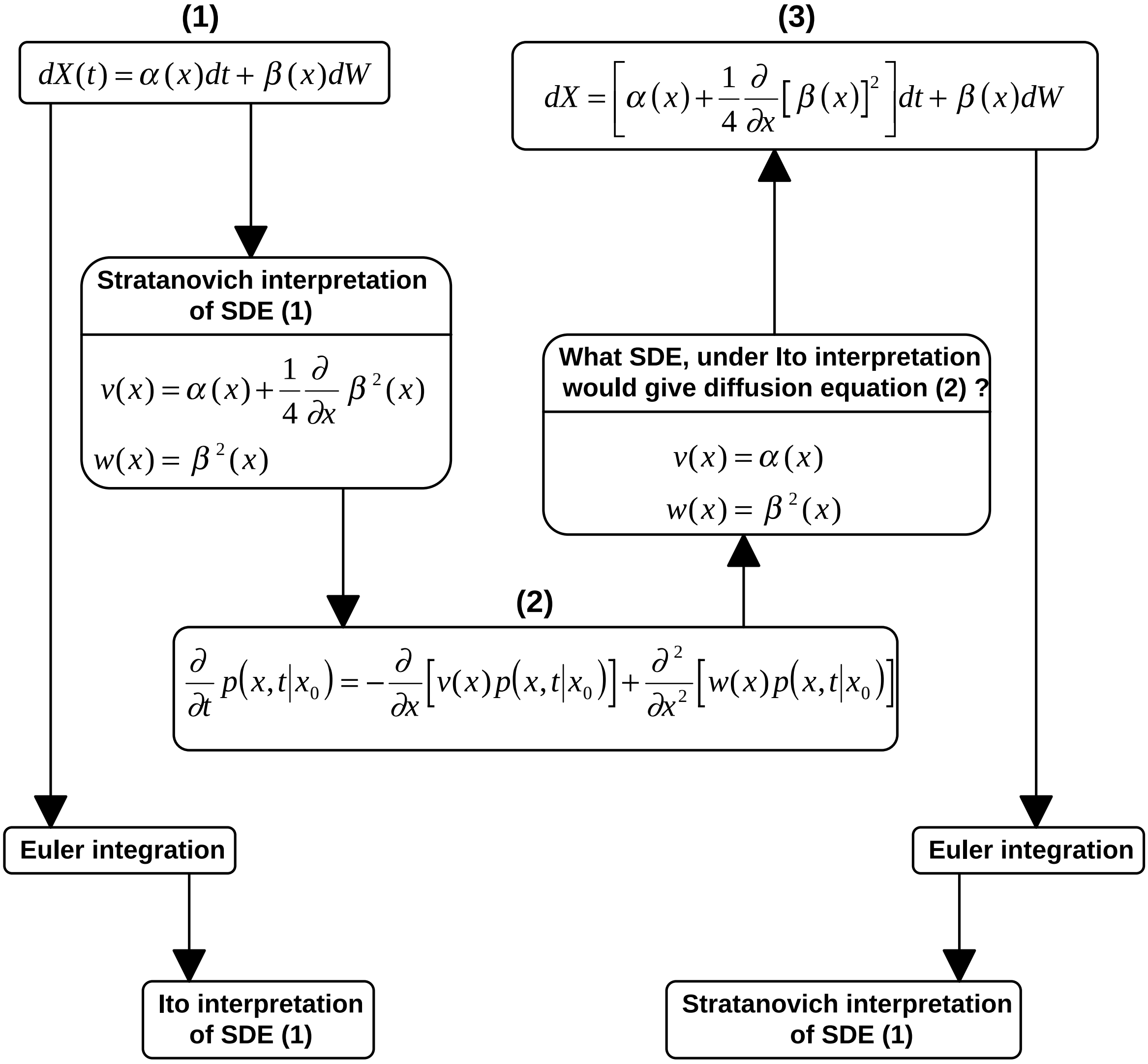


Figure 5.1. Flow chart of steps involved in obtaining both Ito and Stratanovich interpretations of a stochastic differential equation (1) using Euler integration.

Nisbet & Gurney (1982, p.273) urge that the choice of SDE interpretation should be made on ecological rather than mathematical grounds. In the remainder of this section this sound advice is sadly laid to one side: the method of obtaining persistence time results presented below relies on the application of the rules of ordinary calculus. This implies interpreting the stochastic differential equation in the sense suggested by Stratanovich. Turelli (1977) considers the appropriate choice of calculus working on the basis that heuristically derived SDEs such as [5.2] are only ever intended as approximations to biological reality. He concludes that the Stratanovich interpretation is appropriate when the "true" underlying process is a continuous time process subject to continuous noise. Turelli suggests that in most situations in population biology environmental factors are indeed likely to be autocorrelated to some extent, but that underlying process is also characterised by events discrete in time such as seasonal breeding. Where the "true model" is a difference equation subject to autocorrelated noise neither the Ito nor the Stratanovich interpretation is necessarily appropriate. However, Turelli shows that for a suite of simple models the Ito interpretation is generally more biologically reasonable.

It is against this background that the analysis of this section proceeds. From the foregoing paragraphs it may safely be concluded that quantitative estimates of persistence time based on the following should be treated with a fair amount of scepticism. However, I believe that the qualitative conclusions (in particular for the logistic with random carrying capacity) are useful. In the specific cases considered later in this section, the difference that an Ito interpretation of the model would make to the persistence time distribution is considered, and investigated numerically.

Transformation method for persistence time distributions

Consider a stochastic differential equation of the form

$$\frac{dx}{dt} = \alpha(x) + \beta(x)F(t) \qquad [5.6]$$

where $F(t)$ is Gaussian white noise with zero mean and unit variance. Goel & Richter-Dyn (1974) demonstrate the solution of such equations by transformation to simpler equations in a variable z. Dividing the stochastic differential equation [5.6] by $\beta(x)$ gives

$$\frac{dz}{dt} = \hat{v}(z) + F(t) \tag*{[5.7]}$$

where

$$dz = \frac{dx}{\beta(\mathrm{x})} \tag*{[5.8]}$$

and

$$\hat{v}(z) = \frac{\alpha(x(z))}{\beta(x(z))} \tag*{[5.9]}$$

This corresponds to the diffusion equation

$$\frac{\partial k(z|z_0,t)}{\partial t} = -\frac{\partial}{\partial z}\left[\hat{v}(z)k(z|z_0,t)\right] + \frac{1}{2}\frac{\partial^2}{\partial z^2}k(z|z_0,t) \tag*{[5.10]}$$

where $k(z|z_0,t)$ is the probability density function for z. The probability density functions for the untransformed and transformed processes, $p(x|x_0,t)$ and $k(z|z_0,t)$, are linked by the relation

$$k(z|z_0,t) = p(x(z)|x_0,t)\,\beta(x(z)) \tag*{[5.11]}$$

The aim here is to use Goel & Richter-Dyn's transformation method to obtain the probability density function $g(t|x_0,a)$ of the first passage time, T - the time taken for a population initially of size x_0 to reach a lower threshold size of a ($a < x_0$). Following the same procedure as that used in chapter 2, a is represented as an absorbing barrier. Then

$$\begin{aligned}
g(t|x_0,a) &= -\frac{d}{dt}\int_{a^+}^{\infty} p(x|x_0,a,t)dx = -\int_{a^+}^{\infty}\frac{dp(x|x_0,a,t)}{dt}dx \\
&= -\int_{a^+}^{\infty}\left[-\frac{\partial}{\partial x}\big(v(x)p(x|x_0,a,t)\big) + \frac{1}{2}\frac{\partial^2}{\partial x^2}\big(w(x)p(x|x_0,a,t)\big)\right]dx \\
&= -\left[-v(x)p(x|x_0,a,t) + \frac{1}{2}\frac{\partial}{\partial x}\big(w(x)p(x|x_0,a,t)\big)\right]_a^{\infty} = \frac{1}{2}\frac{\partial}{\partial x}\big(w(x)p(x|x_0,a,t)\big)\Big|_a \\
&= \frac{1}{2}\frac{\partial}{\partial x}\left(w(x)\frac{k(z|z_0,b,t)}{[w(x)]^{\frac{1}{2}}}\right)\Bigg|_a
\end{aligned} \tag*{[5.12]}$$

using the relation [5.11] and representing the absorbing barrier for the transformed process z by b.

By the chain rule,

$$\frac{\partial}{\partial x}\left([w(x)]^{\frac{1}{2}}k(z|z_0,b,t)\right)=\frac{\partial}{\partial z}\left([w(x)]^{\frac{1}{2}}k(z|z_0,b,t)\right)\frac{\partial z}{\partial x}$$

and from [5.8] above $\frac{\partial z}{\partial x}=\frac{1}{[w(x)]^{\frac{1}{2}}}$

Thus

$$g(t|x_0,a)=\frac{1}{2}\frac{\partial}{\partial z}k(z|z_0,b,t)\bigg|_{z=b}=g(t|z_0,b) \tag{5.13}$$

where $g(t|z_0,b)$ is the first passage time form z_0 to *b*.

There is, therefore, a very simple relationship between the first passage time distribution for the original process, *x*, and that of the transformed process, *z*.

The logistic model with random variation in the growth rate, *r*

Starting with the differential equation for the deterministic logistic model [5.1] random variation can be introduced into the growth rate, *r*, by replacing the constant by the stochastic form:

$$r(t)=\bar{r}+\sigma F(t) \tag{5.14}$$

where $\bar{r}$ is the mean growth rate with variance σ^2, and *F*(*t*) is Gaussian white noise. This gives the stochastic differential equation

$$\frac{dN}{dt}=\bar{r}N\left(1-\frac{N}{K}\right)+\sigma N\left(1-\frac{N}{K}\right)F(t) \tag{5.15}$$

It should be noted at the outset that this model has some rather strange properties (which will become clear below). However, it seems appropriate to consider it further for two reasons: it is easily obtained (perhaps all to easily) by the heuristic process of allowing one of the parameters in the deterministic logistic to suffer a random "wobble"; and, in addition, this model has already been discussed in the context of risk assessment in population managment by Ginzburg *et al.* (1982), who fail to comment on its peculiarities.

Using the Stratanovich interpretation [5.4] yields the infinitesimal mean and variance for the corresponding diffusion process

$$v(N) = N\left(1 - \frac{N}{K}\right)\left[\bar{r} + \frac{\sigma^2}{2}\left(1 - \frac{2N}{K}\right)\right]$$
$$w(N) = \sigma^2 N^2 \left(1 - \frac{N}{K}\right)^2 \qquad [5.16]$$

In order to produce numerical realisations of the model [5.15] the stochastic differential equation can be rewritten expressing the white noise in terms of the increment of the Wiener process

$$dN = \bar{r}N\left(1 - \frac{N}{K}\right)dt + \sigma N\left(1 - \frac{N}{K}\right)Z(t)\sqrt{dt} \qquad [5.17]$$

Under Euler integration this represents the Ito interpretation of the stochastic differential equation [5.15]. Following the method outlined in Fig. 5.1, the Stratanovich interpretation of [5.15] is obtained by Euler integration of

$$dN = N\left(1 - \frac{N}{K}\right)\left[\bar{r} + \frac{\sigma^2}{2}\left(1 - \frac{N}{K}\right)\right]dt + \sigma N\left(1 - \frac{N}{K}\right)Z(t)\sqrt{dt} \qquad [5.18]$$

Realisations of [5.18] are shown in Fig 5.2 and of [5.17] in Fig 5.3. From these figures it is could perhaps be suggested that the Ito and Stratanovich interpretations

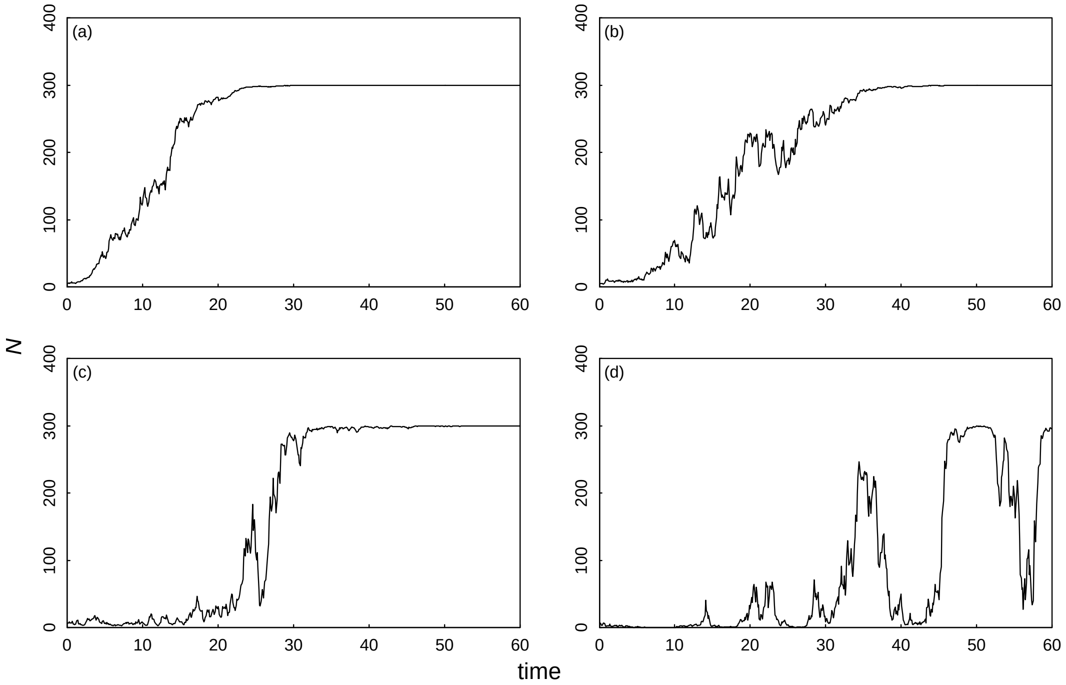


Figure 5.2. Realisations of the logistic with random r, [5.15], using the Stratanovich interpretation (Euler integration of [5.18]). $\bar{r} = 0.3$, $K = 300$. (a) $\sigma^2 = 0.3$, (b) $\sigma^2 = 0.5$, (c) $\sigma^2 = 0.9$, (d) $\sigma^2 = 1.3$.

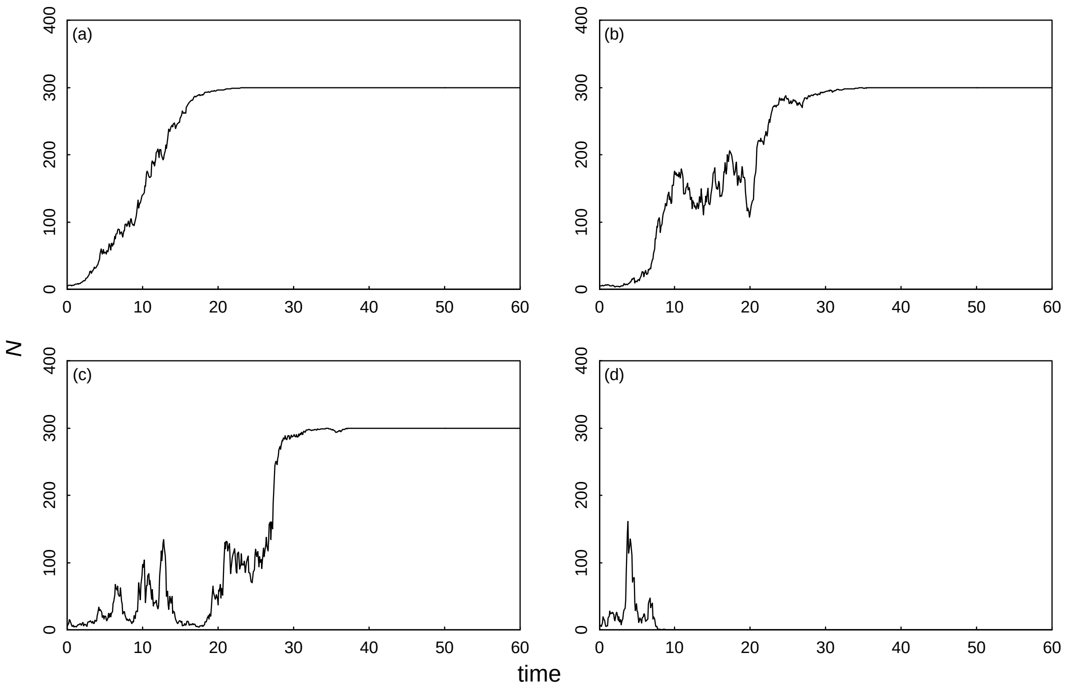


Figure 5.3. Realisations of the logistic with random *r*, [5.15], using the Ito interpretation (Euler integration of [5.17]). $\bar{r} = 0.3$, $K = 300$. (a) $\sigma^2 = 0.3$, (b) $\sigma^2 = 0.5$, (c) $\sigma^2 = 0.9$, (d) $\sigma^2 = 1.3$.

of [5.15] produce broadly similar realisations. In fact, it is possible to be more specific. Where the stochasticity is weak $\left(\sigma^2/2 < \bar{r}\right)$ then under both Stratanovich and Ito interpretations all realisations converge to the close neighbourhood of *K* (Roughgarden 1979). With stronger stochasticity then, under the Ito interpretation, some realisations may alternatively approach zero (in the absence of an absorbing barrier at a larger population size).

The realisations of Figs. 5.2 & 5.3 demonstrate the peculiar feature of the model (obvious from examination of [5.15]) which is that the variance in the population growth rate is affected by the density dependent term, as well as the mean growth rate. Thus, the variance of the growth rate, *r*, approaches zero as the population size approaches the carrying capacity, *K*, which acts as a "built-in" absorbing state (as opposed to the absorbing states imposed, through boundary conditions, on the processes considered in chapter 2). Thus any realisations reaching the vicinity of *K* are trapped there and have no possibility of excursions down to the threshold level. This is probably rather unrealistic from a biological point of view as it is difficult to conceive of mechanisms where the effects of environmental variation on population size are affected to such an extent by population density, and where a population attaining the maximum sustainable size is destined to remain at this level. However, as some of the realisations in Figs. 5.2 & 5.3 demonstrate, the population may fluctuate for some time at sizes below the carrying capacity when the variance in r is large relative to the mean. In such cases (and also perhaps where the carrying capacity is very large) the model, and its persistence time distribution, may be of some interest.

The distribution of population size

Goel & Richter-Dyn (1974) introduce the transformation

$$z = \frac{1}{\sigma}\ln\left[N \Big/ \left(1-\frac{N}{K}\right)\right] \qquad dz = \left[\sigma N\left(1-\frac{N}{K}\right)\right]^{-1} dN \qquad [5.19]$$

in order to obtain the probability density function for N. Rewriting [5.15] in terms of the transformed variable yields the stochastic differential equation

$$\frac{dz}{dt} = \frac{\bar{r}}{\sigma} + F(t) \qquad [5.20]$$

which is the SDE for an unrestricted Wiener process for which the probability density function was given in chapter 2. Using [5.11] and [5.16] gives the probability density function

$$p\left(N \middle| N_0, t\right) = \frac{1}{\sigma (2\pi t)^{\frac{1}{2}} N\left(1-\frac{N}{K}\right)} \exp\left[-\frac{1}{2\sigma^2 t}\left(\ln\left[\frac{N}{N_0}\right] - \ln\left[\frac{\left(1-\frac{N}{K}\right)}{\left(1-\frac{N_0}{K}\right)}\right] - \bar{r}t\right)^2\right] [5.21]$$

To obtain the distribution of times that the population persists above a level N_a it is necessary to consider a lower boundary, b, on the transformed process, z

$$b = \frac{1}{\sigma}\ln\left[N_a \Big/ \left(1-\frac{N_a}{K}\right)\right] \qquad \left(b < z_0\right) \qquad [5.22]$$

such that the transformed process now has diffusion equation

$$\frac{\partial k\left(z \middle| z_0, b\right)}{\partial t} = -\frac{r}{\sigma}\frac{\partial k\left(z \middle| z_0, b\right)}{\partial z} + \frac{1}{2}\frac{\partial^2 k\left(z \middle| z_0, b\right)}{\partial z^2} \qquad [5.23]$$

with boundary condition $k\left(b \middle| z_0, t\right) = 0$.

Using chapter 2 [2.23] the probability density function for the transformed variable in the presence of the lower boundary can easily be found

$$k\left(z \middle| z_o, t\right) = \frac{1}{\sqrt{2\pi t}} \left[\exp\left(\frac{-\left(z - z_0 - \frac{rt}{\sigma} \right)^2}{2t} \right) \right.$$

$$\left. - \exp\left(\frac{2r\left(b - z_0\right)}{\sigma} - \frac{\left(z - 2b + z_0 - \frac{rt}{\sigma} \right)^2}{2t} \right) \right] \qquad [5.24]$$

and again applying the relations [5.11] and [5.16] gives the probability density function for the population size, *N*, in the presence of the lower threshold:

$$p\left(N \middle| N_0, a, t\right) = \frac{1}{\sigma\,(2\pi t)^{\frac{1}{2}}\, N(1 - N/K)}$$

$$\times \left[\exp\left(\frac{-\left(\ln\left[\frac{N}{1 - N/K} \right] - \ln\left[\frac{N_0}{1 - N_0/K} \right] - \bar{r}t \right)^2}{2\sigma^2 t} \right) \right.$$

$$- \exp\left(\frac{2r\left(\ln\left[\frac{N_a}{1 - N_a/K} \right] - \ln\left[\frac{N_0}{1 - N_0/K} \right] \right)}{\sigma^2} \right)$$

$$\left. - \frac{\left(\ln\left[\frac{N}{1 - N/K} \right] - 2\ln\left[\frac{N_a}{1 - N_a/K} \right] + \ln\left[\frac{N_0}{1 - N_0/K} \right] - \bar{r}t \right)^2}{2\sigma^2 t} \right] \qquad [5.25]$$

The persistence time distribution

The persistence time distribution for the transformed variable is the first passage time distribution for the Wiener process, and is again given in chapter 2 [2.24]

$$g\left(t \middle| z_0, b\right) = \frac{z_0 - b}{\sqrt{2\pi t^3}} \exp\left(\frac{-\left(b - z_0 - \frac{\bar{r}t}{\sigma} \right)^2}{2t} \right) \qquad [5.26]$$

Using [5.13] and [5.19], the persistence time distribution for the untransformed processes is obtained simply by substituting

$$z_0 = \frac{1}{\sigma}\ln\left(\frac{N_0}{1-N_0/K}\right), \qquad b = \frac{1}{\sigma}\ln\left(\frac{N_a}{1-N_a/K}\right) \qquad [5.27]$$

Thus the required persistence time distribution is

$$g\left(t\middle|N_0,N_a\right) = \frac{\ln\left(\frac{N_0}{1-N_0/K}\right) - \ln\left(\frac{N_a}{1-N_a/K}\right)}{\sigma\sqrt{2\pi t^3}} \times \exp\left(\frac{-\left(\ln\left(\frac{N_a}{1-N_a/K}\right) - \ln\left(\frac{N_0}{1-N_0/K}\right) - \bar{r}t\right)^2}{2\sigma^2 t}\right) \qquad [5.28]$$

This corresponds with the result previously obtained by Ginzburg *et al.* (1982) for the logistic with random r (but who fail to mention the necessity of assuming a Stratanovich interpretation in order to make the required transformations to the Wiener process). In Fig. 5.4 the persistence time distribution given by [5.28] is compared with distributions obtained numerically by Euler integration of [5.17] and [5.18]. In these cases the persistence time distributions resulting from Ito and Stratanovich interpretations of [5.15] are in fact very similar, despite the fact that $\sigma^2/2 > \bar{r}$ in three of the four examples. The persistence time distribution of [5.28], not surprisingly, gives a slightly better fit to the distributions obtained using a Stratanovich interpretation. Nevertheless, in the examples illustrated at least, the Ito case is approximated by [5.28] extremely well. In Fig. 5.4b to d the Ito interpratation results in a slightly higher probability of reaching the lower threshold at short times. This is presumably due to the fact that in these cases the Ito interpretation results in some realisations approaching zero rather than the carrying capacity, *K*.

Because the persistence time distribution [5.28] is simply the first passage time distribution of a scaled Wiener process, many of the results of chapter 2 are again available.

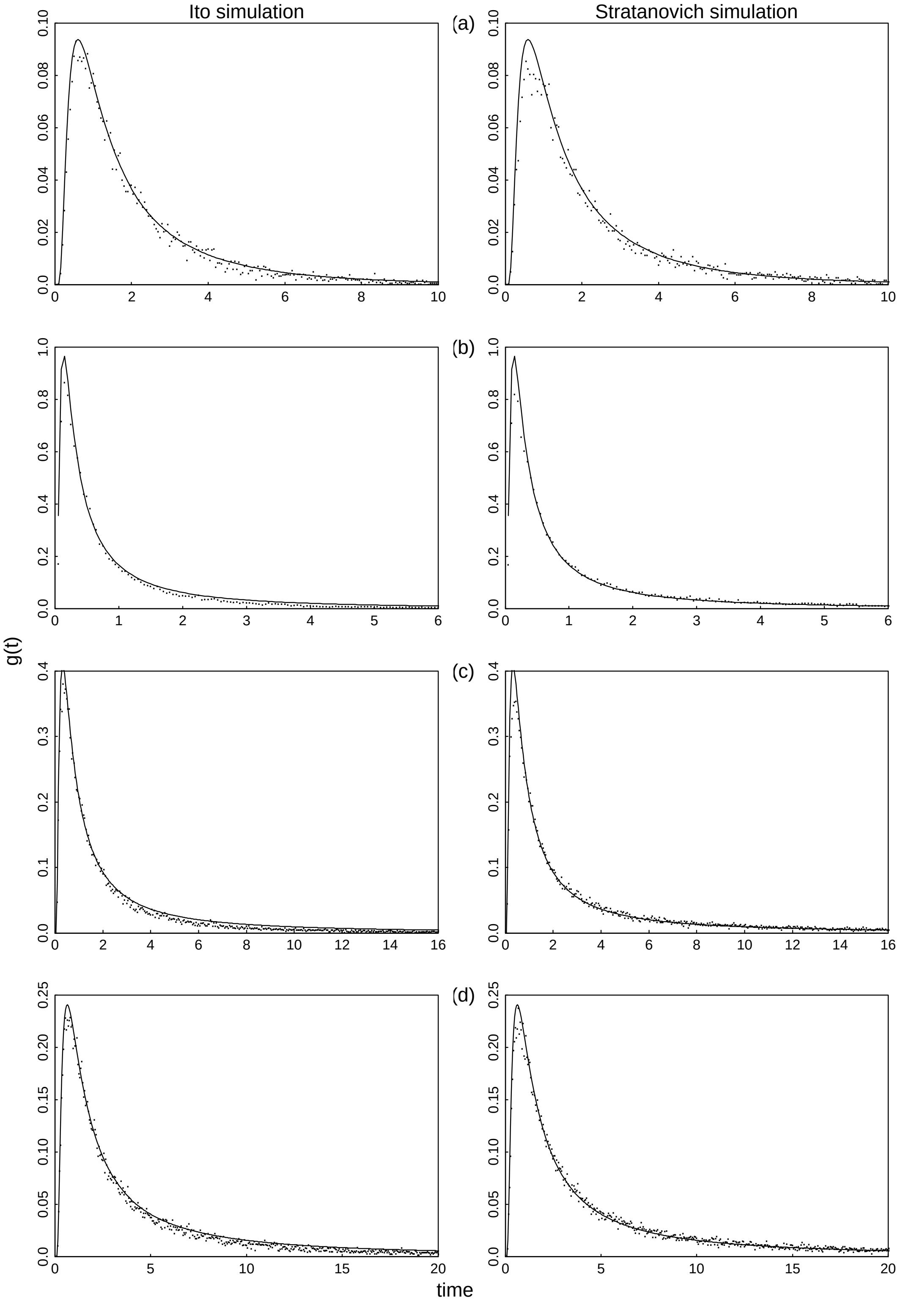


Figure 5.4. Persistence time distributions obtained by Euler integration of [5.18] (Stratanovich interpretation of [5.15]) and [5.17] (Ito interpretation of [5.15]). Lines from persistence time distribution [5.28], obtained by transformation method. (a) $\overline{r} = 0.3$, $\sigma = 0.5$, $K = 300$, $N_0 = 150$, $N_a = 100$; (b) $\overline{r} = 0.3$, $\sigma = 1.1$, $K = 300$, $N_0 = 150$, $N_a = 100$; (c) $\overline{r} = 0.1$, $\sigma = 0.7$, $K = 300$, $N_0 = 150$, $N_a = 100$; (d) $\overline{r} = 0.0$, $\sigma = 0.5$, $K = 300$, $N_0 = 150$, $N_a = 100$.

The probability of ultimately reaching the lower threshold is given by

$$G\left(\infty \middle| N_0, N_a\right) = \begin{cases} 1 & (\bar{r} \le 0) \\ \exp\left(-\frac{2\bar{r}}{\sigma^2}\left(\ln\left(\frac{N_0}{1 - N_0 / K}\right) - \ln\left(\frac{N_a}{1 - N_a / K}\right)\right)\right) & (\bar{r} > 0) \end{cases} \qquad [5.29]$$

As the model [5.15] is really only of any interest when $\bar{r}$ is non negative, there will always be a finite probability that the lower threshold is not reached (Ginzburg *et al.* (1982) consider cases where $\bar{r}$ is negative without apparently realising the biological absurdity of a model where the density dependent effect is to *decrease* the mean growth rate as the population get smaller). In contrast, however, to the linear model of chapter 2, this is not due to the fact that populations are attaining infinite size, but rather to the fact that realisations are trapped at the built-in absorbing barrier at *K*.

The mean persistence time, conditional on reaching the threshold, is given by

$$\text{mean} = \frac{\left(\ln\left(\frac{N_0}{1 - N_0 / K}\right) - \ln\left(\frac{N_a}{1 - N_a / K}\right)\right)}{\bar{r}} \qquad [5.30]$$

Thus the mean persistence time is unaffected by the variance in the population growth rate, and an increased mean growth rate leads to decreased mean persistence times. This is because as $\bar{r}$ is increased it becomes increasingly easy for realisations to reach the carrying capacity, and the only realisations reaching the threshold are those that experience a run of low growth rates early in the realisation. This is essentially the same reason that increasing positive long run growth rates, μ, in the linear model led to shorter mean persistence times. The modal persistence time is given by

$$\text{mode} = \begin{cases} \dfrac{\left(\ln\left(\dfrac{N_0}{1-N_0/K}\right)-\ln\left(\dfrac{N_a}{1-N_a/K}\right)\right)^2}{3\sigma^2} & (\bar{r}=0) \\[2ex] \dfrac{1}{\bar{r}}\left(\ln\left(\dfrac{N_0}{1-N_0/K}\right)-\ln\left(\dfrac{N_a}{1-N_a/K}\right)\right) & \\ \times\left(1+\dfrac{9\sigma^4}{4\bar{r}^2\left(\ln\left(\dfrac{N_0}{1-N_0/K}\right)-\ln\left(\dfrac{N_a}{1-N_a/K}\right)\right)^2}\right)^{\frac{1}{2}}-\dfrac{3\sigma^2}{2\bar{r}^2} & (\bar{r}>0) \end{cases} \qquad [5.31]$$

Like the mean persistence time, the mode falls as the mean growth rate is increased (Fig 5.5). However, in contrast to the expected persistence time, the modal persistence time is affected by the magnitude of the variation in growth rate. This is illustrated in Fig. 5.6 which demonstrates that increased variance in the growth rate produces a reduction in modal persistence time.

Figure 5.7 investigates the change in mean and modal persistence time as the carrying capacity, *K*, is increased. Both mean and mode decrease, accompanied by an increasing ultimate probability of reaching the lower threshold. These changes appear to be due to the fact that increasing the carrying capacity means that the "safe state" that *K* represents is further away from the initial population size and the population is, therefore, more likely to reach the lower threshold.

Discussion

Examination of the logistic model with random growth rate demonstrates that it is possible to get exact results for the models persistence time distribution by transformation to a simpler stochastic process for which results are available. Unfortunately the method relies on assuming a Stratanovich interpretation of the model's stochastic differential equation, thought the simulations carried out suggest that persistence time under an Ito interpretation is broadly similar.

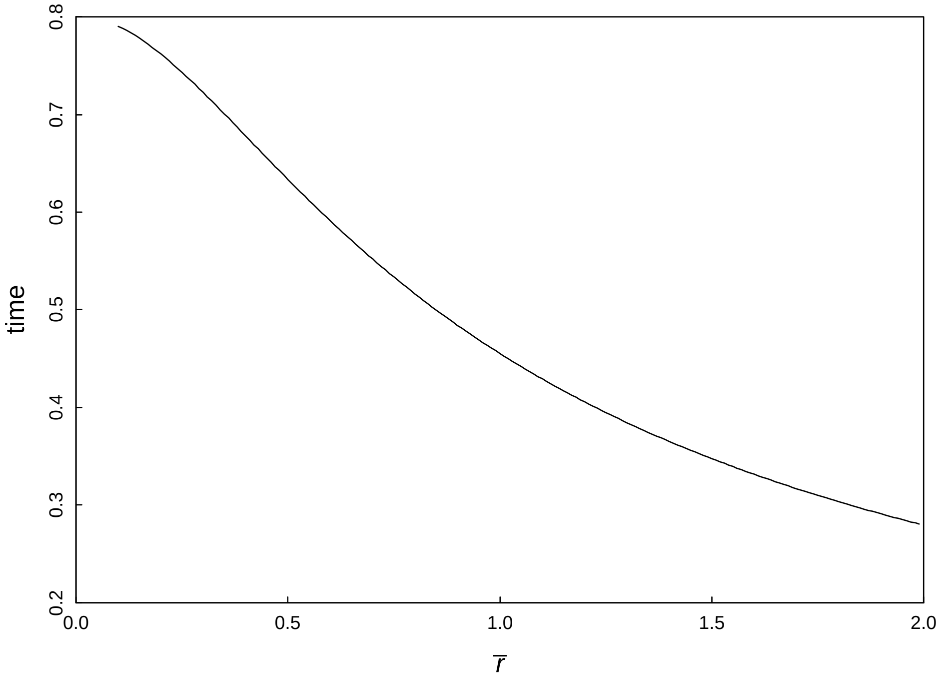


Figure 5.5. Modal persistence time (from [5.31]) in the logistic with random r as $\bar{r}$ is increased. $\sigma^2 = 0.2$, $K = 300$, $N_0 = 150$, $N_a = 100$.

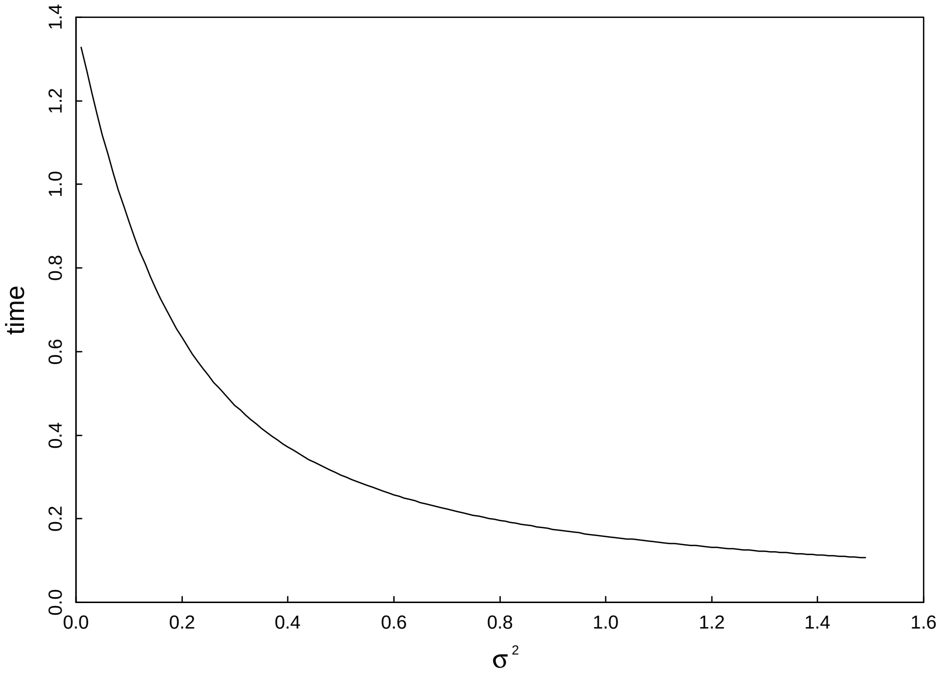


Figure 5.6. Change in modal persistence time as the variance in growth rate (σ^2) is increased. $\bar{r} = 0.5$, $K = 300$, $N_0 = 150$, $N_a = 100$.

However, many aspects of the persistence time distribution considered here can be attributed to the rather peculiar situation caused by the built in absorbing state at the carrying capacity, *K*. This effectively guarantees persistence to any realisation attaining a population size near *K*, due to the fact that variation in the growth rate decreases with population size. This feature would seem to have more to do with the way in which environmental variance has been incorporated in the model than biological reality. It would, therefore, be rather imprudent to attach any biological significance to the persistence time results obtained here. The issue of whether the Ito or Stratanovich calculus is appropriate is rather less important than recognition of the fact that this simple extension of the deterministic logistic model sheds little light on the issue of persistence in regulated populations.

Logistic model with random carrying capacity, *K*

The logistic model with random *r* considered above was applicable, at best, to a population growing from a level well below the carrying capacity. Because the variation in *r* was density dependent the absurd situation was produced where any

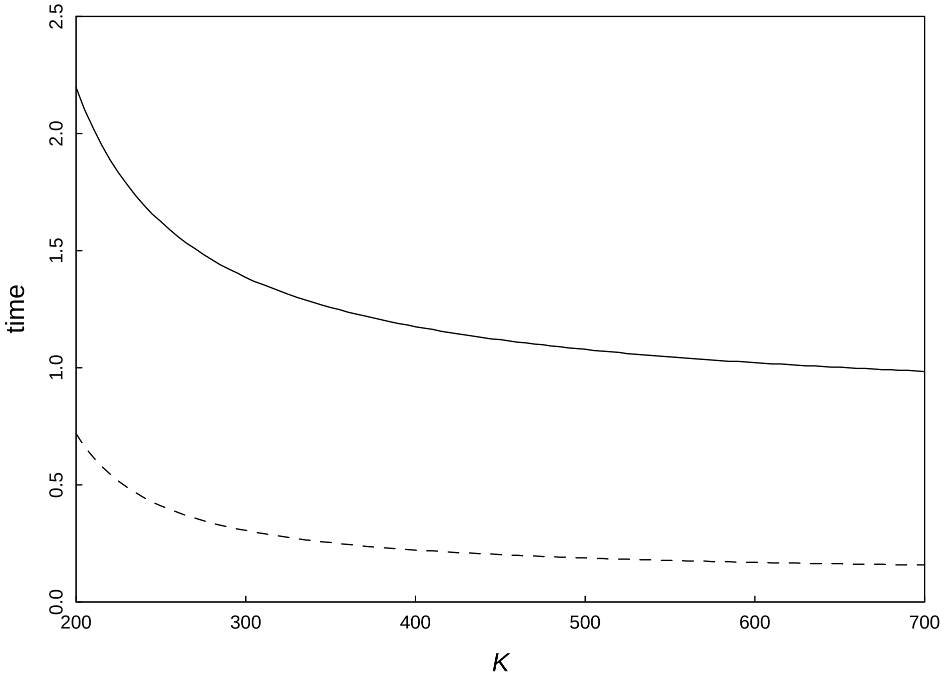


Figure 5.7. Mean (—) and modal (--) persistence time as a function of *K*. $\bar{r} = 0.5$, $\sigma^2 = 0.5$, $N_0 = 150$, $N_a = 100$.

population growing to near the level of the carrying capacity persisted indefinitely. Here the other possible stochastic extension of the simple logistic is considered, namely where the carrying capacity is affected by environmental variation. This situation is likely to be of greater interest in a management context than the logistic model with random *r*, because the census data available for populations often shows an average growth rate around zero, but are insufficient to distinguish whether the population is unregulated with a low growth rate, or fluctuating around some "equilibrium" size. It is therefore of interest to understand the differences between presistence in a model with varying carrying capacity, and persistence in a linear model with a low growth rate.

Fluctuations in the carrying capacity must be introduced into the logistic model [5.1] through a function linear in K (Roughgarden 1979, p.379). Following Goel & Richter-Dyn (1974) this is done by defining $M(t)$, where

$$M(t) = \frac{1}{K(t)} \qquad [5.32]$$

Then fluctuations are introduced in M such that $M(t) = \overline{M} + \sigma_M F(t)$. Substituting in the original deterministic logistic model [5.1] leads to the stochastic differential equation

$$\frac{dN}{dt} = rN - rN^2\left[\overline{M} + \sigma_M F(t)\right] \qquad [5.33]$$

In order to investigate the distribution of population size, Goel & Richter-Dyn introduce the transformation

$$z = \frac{\left(1/N - \overline{M}\right)}{\sigma_M r} \qquad [5.34]$$

The transformed variable, z, has the stochastic differential equation

$$\frac{dz}{dt} = -rz + F(t) \qquad [5.35]$$

This is the SDE for an Ornstein-Uhlenbeck process. Goel & Richter Dyn (1974) and Levins (1969) show that asymptotically, as $t \to \infty$, the reciprocal of population size, $1/N$, is normally distributed with mean $\overline{M}$ and variance

$$\frac{1}{2\sigma_M^2 r} \qquad [5.36]$$

Realisations of the model [5.33] (Fig. 5.8) again show a certain amount of similarity between the Ito and Stratanovich interpretations. However differences do exist, dicussed by Turelli (1977) and Roughgarden (1979). The infintesimal means for the associated diffusion processes are

$$\begin{aligned} v(x) &= rN - r\overline{M}N^2 && \text{Ito interpretation} \\ v(x) &= rN - r\overline{M}N^2 + \sigma^2 r^2 N^3 && \text{Stratanovich interpretation} \end{aligned} \qquad [5.37]$$

The extra term under the Stratanovich interpretation means that, despite the density dependent regulation, explosion to infinite population sizes can take place. The

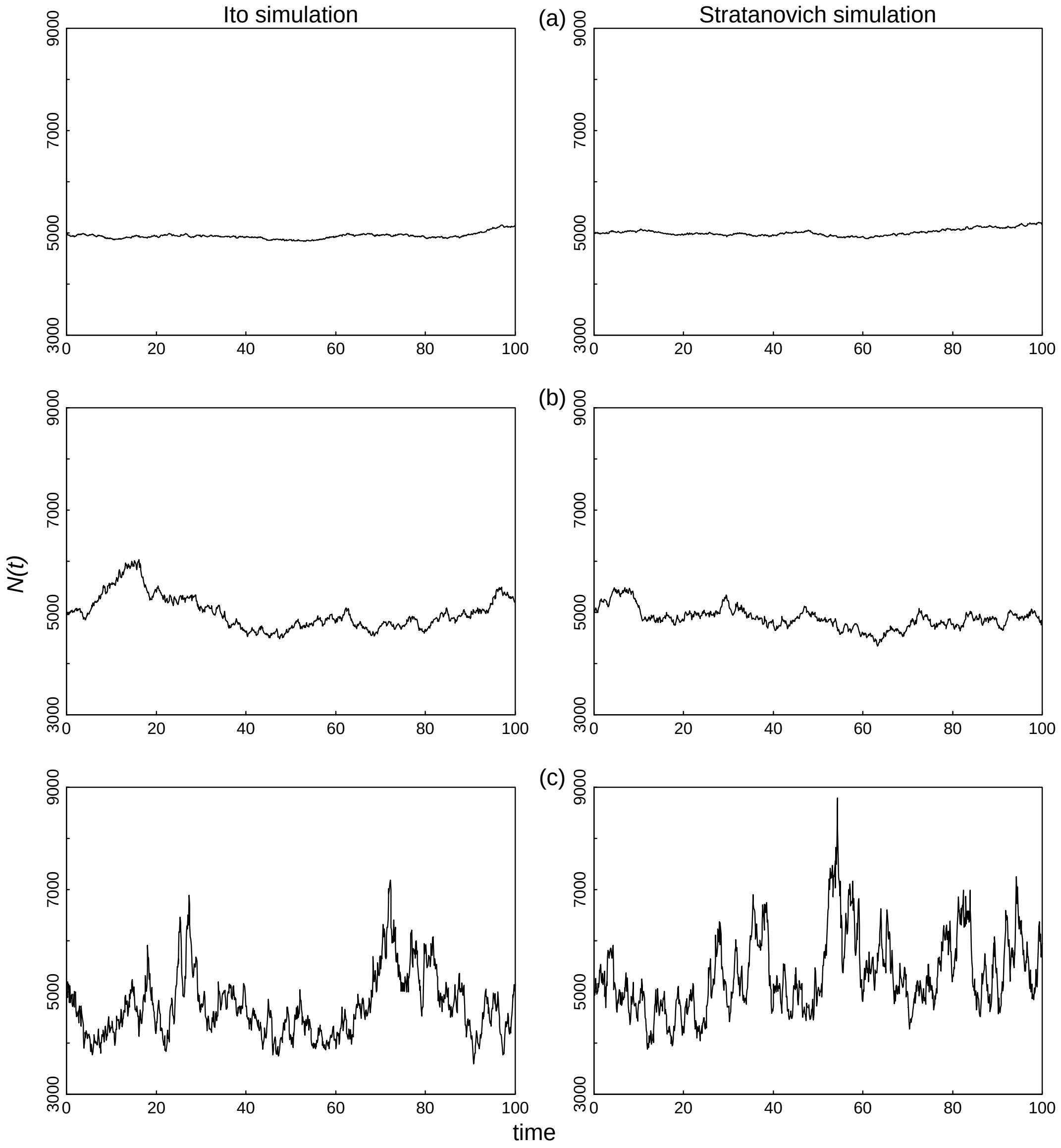


Figure 5.8. Realisations of the logistic with random variation in the carrying capacity. Stratanovich interpretation obtained by Euler integration of [5.40], Ito interpretation using [5.39]. $\overline{M}$ = 0.0002, σ_M = 0.00009, N_0 = 5000. (a) r = 0.01; (b) r = 0.05; (c) r = 0.25.

model itself is also not without problems. As the range of the random variable is not restricted negative carrying capacities may also arise on occasions, in which case the model becomes an undamped quadratic growth model (Turelli 1977). The persistence time results that follow are therefore only likely to be of interest when the carrying capacity, and its variance, are not too large.

Persistence time

As the transformed variable, z, is described by an Ornstein-Uhlenbeck process, results for the persistence time are again available in chapter 2. In particular, the mean persistence time of a population initially of size N_0 above a lower threshold size, N_a, is given by

$$\begin{aligned} E\left(T\middle|N_0, N_a\right) = \frac{1}{r}\Bigg[\frac{1}{2}\Bigg(\psi\left[\frac{(2r)^{\frac{1}{2}}}{\sigma_M r}\left(\frac{1}{N_a}-\overline{M}\right)\right]-\psi\left[\frac{(2r)^{\frac{1}{2}}}{\sigma_M r}\left(\frac{1}{N_0}-\overline{M}\right)\right]\Bigg) \\ +\left(\frac{\pi}{2}\right)^{\frac{1}{2}}\Bigg(\chi\left[\frac{(2r)^{\frac{1}{2}}}{\sigma_M r}\left(\frac{1}{N_0}-\overline{M}\right)\right]-\chi\left[\frac{(2r)^{\frac{1}{2}}}{\sigma_M r}\left(\frac{1}{N_a}-\overline{M}\right)\right]\Bigg)\Bigg] \end{aligned} \qquad [5.38]$$

where $\psi(x)$ and $\chi(x)$ are defined in [2.51].

Again, numerical simulations can be used to check the extent to which the Ito interpretation of the stochastic differential equation [5.33] differs from the mean persistence time based on a Stratanovich interpretation. Realisations of the model [5.33] using an Ito interpretation of the Wiener increment are obtained by Euler integration of

$$\frac{dN}{dt} = rN - rN^2\overline{M} - rN^2\sigma_M Z(t)\sqrt{dt} \qquad [5.39]$$

while Stratanovich realisations are obtained by Euler integration of

$$\frac{dN}{dt} = rN - rN^2\overline{M} + \sigma^2 r^2 N^3 - rN^2\sigma_M Z(t)\sqrt{dt} \qquad [5.40]$$

Table 5.1 compares mean persistence times for the logistic with a randomly varying carrying capacity [5.33] given by [5.38] with numerical estimates using both the Stratanovich and Ito interpretations of [5.33]. The mean persistence time obtained by the transformation method is close to the numerical estimates obtained under both Ito and Stratanovich interpretations. However, given that [5.38] is an exact result for the Stratanovich interpretation, it is noticeable that the corresponding numerical estimates produce a slightly longer mean persistence time. The explanation for this discrepancy is associated with the problems of numerical simulation, in particular the

Table 5.1. Mean persistence times given by [5.38] compared with persistence times estimated under Ito (Euler integration of [5.39]) and Stratanovich (Euler integration of [5.40]) interpretations of the logistic with randomly varying carrying capacity [5.33].

						Expected persistence time		
						Exact result	Numerical estimates	
	r	$\overline{M}$	σ_M	N_0	N_a	[5.38]	Ito	Stratanovich
(a)	0.5	0.01	0.002	100	90	5.0186	5.0531	6.6532
(b)	0.5	0.01	0.002	100	85	14.055	13.108	17.252
(c)	0.5	0.01	0.002	100	80	54.028	45.676	64.066
(d)	0.9	0.01	0.002	100	85	3.8469	3.6983	4.9285
(e)	0.5	0.01	0.005	100	85	2.4705	1.9628	3.1210

use of a fixed time step producing a discrete approximation to the continuous model. These problems are discussed further in the next section (where local linearisation methods are used in the estimation of persistence time in a discrete time logistic model). For the present it should be noted that the main difference between the Stratanovich and Ito interpretations is that the mean persistence time is generally less under the Ito interpretation, a fact that results from the diffusion process under a Stratanovich interpretation having a larger infintesimal mean at smaller population sizes (Turelli 1977).

Using the result of Nobile, Ricciardi & Sacerdote (1985) (see chapter 2 [2.48]) it should be possible, for large times, to approximate the probability density function of the persistence time distribution as

$$g(t|N_0, N_a) = \frac{1}{E(T|0, N_a)} \exp\left(-\frac{t}{E(T|0, N_a)}\right) \qquad [5.41]$$

where $E(T|0, N_a)$ is given by [5.38] above. This has been done for several of the numerical persistence time distributions that were estimated in order to provide the mean persistence time estimates of Table 5.1. The results are shown in Fig. 5.9 and demonstrate that, for these examples, [5.41] provides an useful approximation to the distribution of persistence times for most of the distribution, with the exception of t small.

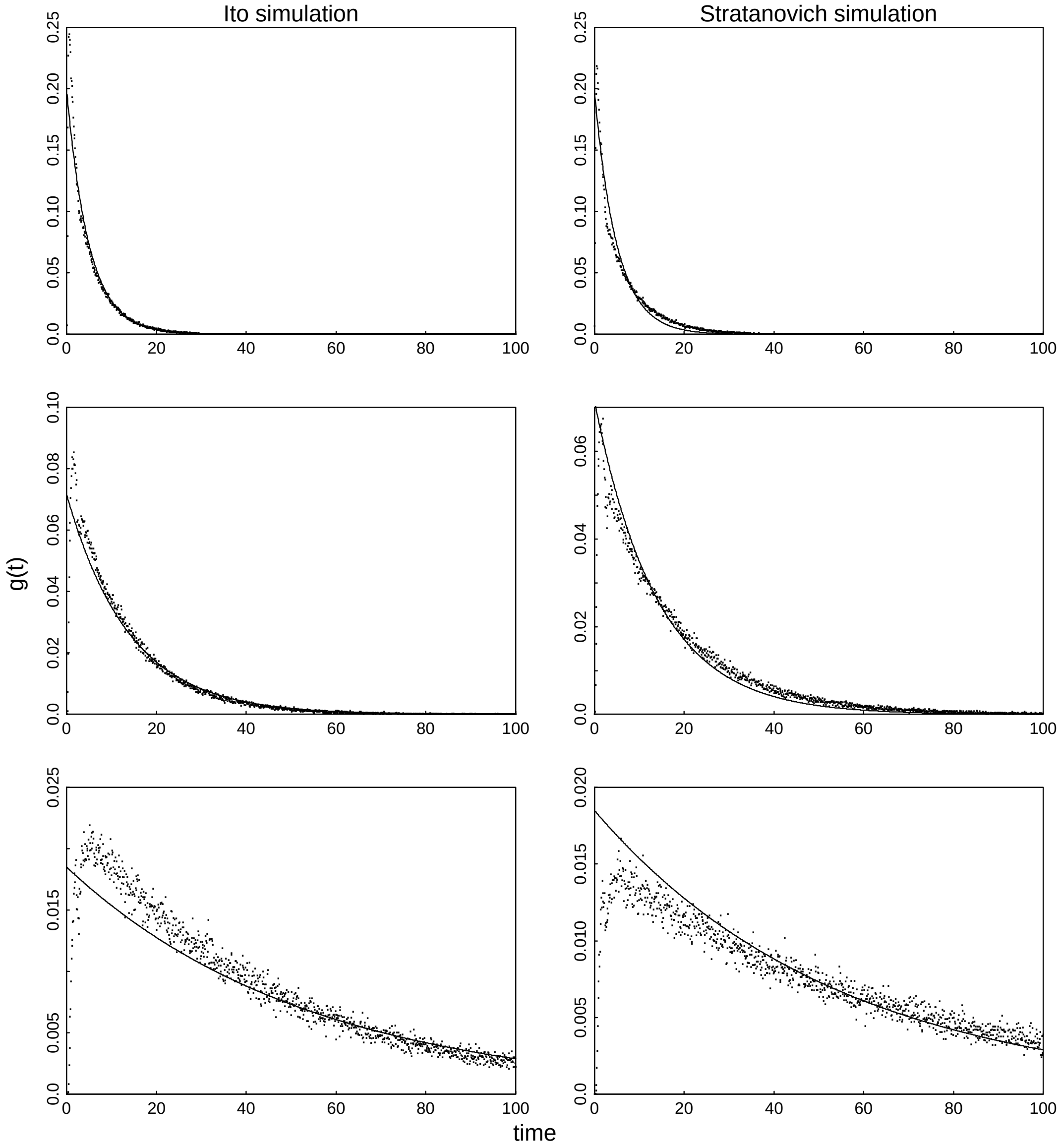


Figure 5.9. Numerical estimates of the persistence time distribution of the logistic with random K under both Ito and Stratanovich interpretations (obtained by Euler integration of [5.39] and [5.40] respectively) with lines showing the approximated distribution given by [5.41]. Parameters given in Table 5.1 (a to c).

Features of the persistence time distribution

Figs. 5.10, 5.11 and 5.12 investigate the effect on the expected persistence time of changes in one of the parameters of the model. Fig. 5.10 demonstrates that an increased population growth rate, r, actually leads to a rapidly declining expected persistence time in the logistic with random carrying capacity. This is because a higher growth rate leads to greater variance in population size [5.36] (Fig. 5.8). This

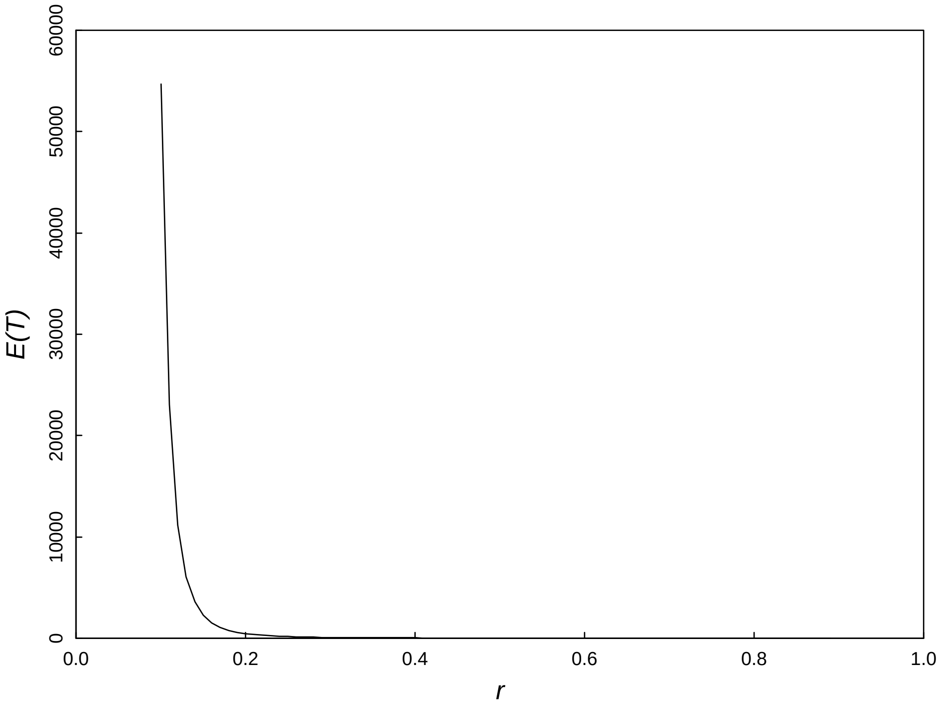


Figure 5.10. Mean persistence time for the logistic with randomly varying carrying capacity as *r* is increased. $\bar{M} = 0.002$, $\sigma_M = 0.00009$, $N_0 = 5000$, $N_a = 3500$.

can be attributed to the higher growth rate making the population size more reactive to changes in the carrying capacity. Goel & Richter-Dyn (1974) give the most probable (i.e. modal) population size as $1/\overline{M} - \sigma^2 r / \overline{M}^3$. Modal population size is thus reduced by an increased growth rate, a fact which will also contribute to the decreased expected persistence time.

It is clear from [5.36] and the expression given above for modal population size that the variance in the carrying capacity, σ_M^2, acts in a similar way to the population growth rate, *r*. Therefore increased environmental variation in the carrying capacity reduces the expected persistence time of the population. This is illustrated in Fig 5.11.

Fig. 5.12 demonstrates the difference in expected persistence time for different lower threshold values, given a constant growth rate and constant carrying capacity mean and variance. For lower thresholds fairly near to the mean carrying capacity expected persistence times are, of course, short. As lower thresholds are considered the expected persistence time increases rapidly .

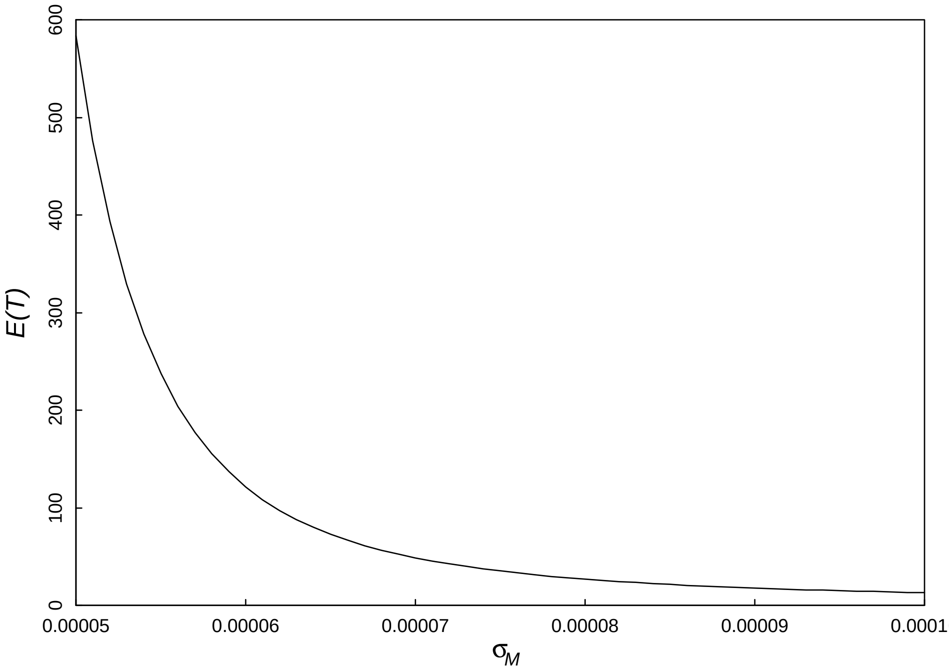


Figure 5.11. Mean persistence time for the logistic with randomly varying carrying capacity as the variation in the carrying capacity increased. $r = 0.5$, $\bar{M} = 0.002$, $N_0 = 5000$, $N_a = 3500$.

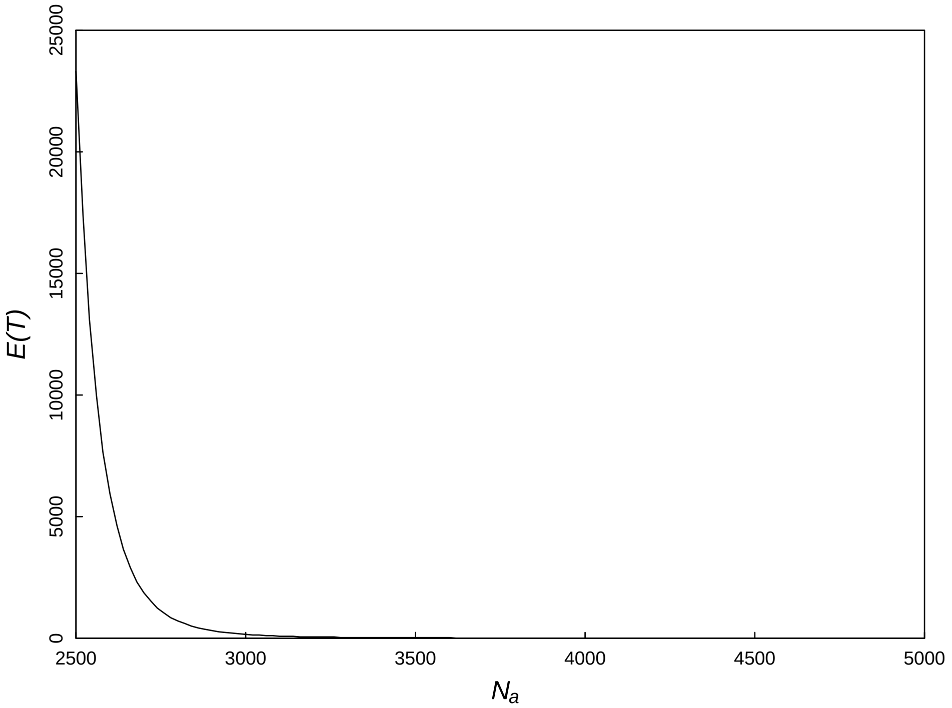


Figure 5.12. Mean persistence time for the logistic with randomly varying carrying capacity as the lower threshold is increased. $r = 0.5$, $\bar{M} = 0.002$, $\sigma_M = 0.00009$, $N_0 = 5000$.

Discussion

The model considered here, with a randomly fluctuating carrying capacity, is of rather more interest than the previous model with fluctuations introduced into *r*. However, as mentioned earlier, this model is not without problems resulting both from the enforced Stratanovich interpretation and the easy, but rather non-rigorous, method of producing a stochastic logistic by simply adding noise to a parameter of the deterministic logistic model. For instance, as found numerically in Table 5.1, an Ito interpretation of the SDE [5.33] produces a shorter expected persistence time. Despite this, the general, qualitative, features of the persistence time distribution investigated here probably represent the features that would arise in a wide range of density dependent models where the population size fluctuates around some mean value or "equilibrium" size. It is reasonably intuitive that in such situations an exponential distribution persistence of persistence times should arise. This reflects the fact that particularly poor sequences of environmental conditions, causing the population to leave the 'normal' range of sizes and reach a lower threshold, should arise more or less randomly in time. In addition, the rapid increase in expected persistence time as smaller threshold levels are considered is consistent with the fact that the probability that a regulated population has an excursion to a low level should decrease rapidly as the level considered becomes further removed from the populations normal range, as given, for instance, by the standard deviation of the population distribution.

While an exponential persistence time distribution seems likely in most situations where there is some mean or "equilibrium" population size around which the population fluctuates in a more or less bounded manner, it must be emphasised that such a situation is not necessarily an inevitable outcome of a non-linear (density dependent) model. There are, of course, many instances where (deterministic) non-linear models have cyclical or chaotic dynamics rather than a point equilibrium, as is the case with the deterministic logistic model. Introducing stochasticity into models other than those where the deterministic case has a point equilibrium may produce rather different persistence time results than those presented here. If, for instance, a population exhibits fluctuations in size largely bounded around a cyclically varying mean, the persistence time distribution is unlikely to be unimodal. Nisbet & Gurney (1982, p.228) show the stepped shape of the curve of probability that extinction has occured, against time, for one such cyclical model.

Ginzburg, Ferson & Akçakaya (1990) carried out a simulation study of the effect of density dependence on persistence. Using a single functional form, the Ricker stock recruitment curve, the found that weak to moderate density dependence generally extended persistence time but strong density dependence shortened persistence times, relative to the density independent case. The reason for this is that the weaker density dependence produces point equilibria in the deterministic case, but stronger density dependence produces cyclical behaviour. The additional fluctuations in population size due to environmental stochasticity means that models with a cyclic deterministic equilibrium may have a greater probability of reaching some low threshold size than those models where population growth rate is independent of population size.

It was suggested previously that in applied situations the situation may often arise where a population seems to be fluctuating around some level but where, due to limitations on the data available, it is not possible to say whether the population is regulated or whether it just has a very low growth rate. The data available for the acorn woodpecker population considered at the end of chapter 4 in fact provided fairly clear evidence that the population was regulated in a density dependent manner. The linear model with an upper barrier suggested that in the absence of immigration or density dependent reproduction or survival the most likely persistence time of the population would be quite short. Stacey & Taper (1992) suggest that much of the variation in population size in the woodpecker population can be attributed to the annual variation in the production of acorns, the populations overwinter food supply. Stacey (1979) described how birds may be forced to leave the study canyon by a small acorn crop. Such a fluctuating resource level is of course an example of a varying carrying capacity so it is of interest to consider the data in the light of the model presented here and compare the persistence time distributions obtained with those suggested by the linear model applied previously. It must be emphasised however that the continuous time model considered here is far from the most appropriate model for the acorn woodpecker population. The woodpeckers reproduce seasonally (in the spring of each year) and reproduction is thus temporally distinct from the main impacts of the fluctuating resource levels. In addition the parameters of the logistic model with a fluctuating carrying capacity are not readily equated with the demographic parameters measured by Stacey & Taper. Proceeding with these caveats in mind the parameters of [5.33] may be crudely fitted to the data of Table 4.1 yielding estimates of $r = 1.0023$, $\overline{M} = 0.024$, $\sigma_M^2 = 0.0001$. Realisations of the model with these parameters are shown in Fig. 5.13.

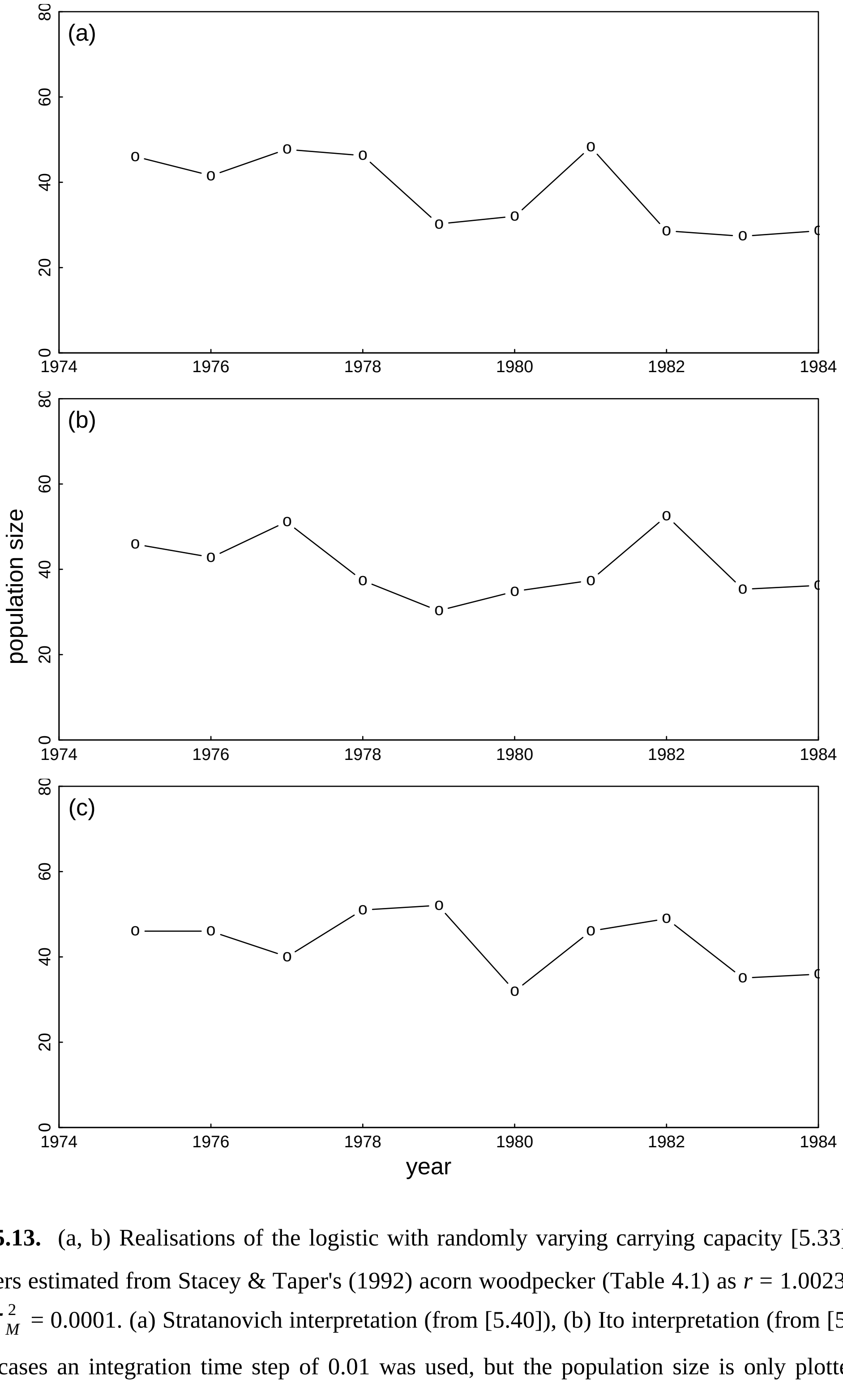


Figure 5.13. (a, b) Realisations of the logistic with randomly varying carrying capacity [5.33] with parameters estimated from Stacey & Taper's (1992) acorn woodpecker (Table 4.1) as r = 1.0023, $\bar{M}$ = 0.024, σ_M^2 = 0.0001. (a) Stratanovich interpretation (from [5.40]), (b) Ito interpretation (from [5.39]). In both cases an integration time step of 0.01 was used, but the population size is only plotted for

yearly intervals. The actual population size recorded by Stacey & Taper in the spring of each year is shown in (c).

Despite the problems noted above the model, with these parameters, produces realisations which are similar in appearance to the observed series of population sizes. In Fig 5.14 the expected persistence time for the logistic with varying carrying capacity (with the parameters fitted to Stacey & Taper's (1992) data) is compared with the expected persistence time for the linear model with a hard upper limit of 52 individuals, and parameters including the effect of immigration, described at the end of chapter 4. It is obvious from this figure that the density dependent model has much greater mean persistence times for lower threshold levels. For instance, the logistic considered here has an expected persistence time of 1.34E+24 years above a threshold of 10 individuals, whereas the linear model with an upper limit of 52 individuals and parameters incorporating the effect of immigration has an expected persistence time above the same threshold level of only about 11 years. Density dependent regulation thus has a major effect in prolonging persistence times in this situation.

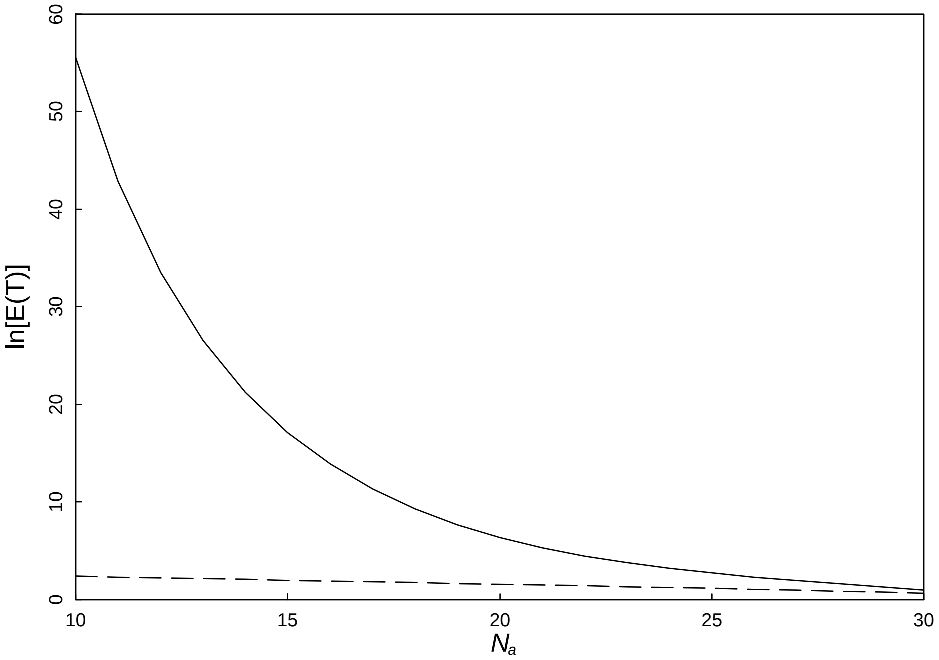


Figure 5.14. The natural logarithm of expected persistence time for the logistic with varying carrying capacity (r = 1.0023, $\bar{M}$ = 0.024, σ_M^2 = 0.0001, solid line), and the linear model with an upper limit ($\bar{\lambda}$ = 0.955, Var(λ) = 0.109, N_b = 52, dashed line) for a range of lower threshold values. The initial population size is 52 for both models.

Applying local linearisation in the estimation of persistence time

While the previous sections have demonstrated that exact solutions to some aspects of the persistence time problem are possible for certain non-linear population models, the methods used are not really very general and unfortunately are constrained somewhat by the problem of different interpretations of stochastic differential equations. A technique that has enjoyed great success in determining the stability properties of deterministic models (Maynard-Smith 1974, May 1974, Nisbet & Gurney 1982), and estimation of moments in stochastic models (Nisbet & Gurney 1982, ch7, Nisbet, Gurney & Pettiphar 1977), is local linearisation.

Several authors (McNeil & Schach 1973, Chesson 1982, Nisbet & Gurney 1982, Turelli 1986) have pointed out that many continuous time stochastic population models which incorporate density dependence give rise to an Ornstein-Uhlenbeck (OU) process when linearised around the mean. Similarly, many discrete time models give rise to an autoregressive process [Renshaw (1987) discusses the connection between the OU process and autoregressive processes]. As first passage time results for the OU process are available (see chapter 2) it is worth considering whether this is a useful route for investigation.

The first question that must be considered is whether persistence time in the full non-linear model is adequately reflected by that of the locally linear approximation. Locally linear models specifically consider infinitely small deviations from the population mean (or from the equilibrium when the stability of a deterministic model is under investigation). While this has proved to be a very robust technique in some instances, there is good reason to suppose that its use in the determination of persistence times may be more limited. Given that the lower threshold for which the persistence time distribution is sought is generally somewhat smaller that the mean population size, and probably outwith the "normal" range of population size, then the events which lead to the arrival of a population trajectory at the lower threshold involve deviations from the mean of some magnitude, and may therefore not be reflected adequately in the locally linear approximation.

A logistic model and a linear approximation

A simple way to discover whether the persistence time distribution of the locally linear model is an adequate representation of that of the full model is, of course, to simply compare the two. Here the numerically derived passage time distributions for a full, non linear, stochastic model and its linearisation are compared. The model considered is a discrete time model, as this is less computationally intensive. Its linearisation is therefore an autoregressive, rather than an OU, process. Nevertheless, in the first instance it allows the testing of the concept of whether a locally linear model can adequately reproduce the persistence time distribution of the non-linear model it approximates. The model investigated here is the discrete time stochastic logistic of Roughgarden (1975).

Roughgarden considers the discrete logistic with constant intrinsic rate of increase, *r*, and random carrying capacity, K_t:

$$N_{t+1} = \left(r + 1 - \frac{r}{K_t} N_t \right) N_t \qquad [5.42]$$

Introducing n_t and k_t as the deviation from the deterministic equilibrium population size ($\overline{N}$) and mean carrying capacity ($\overline{K}$) respectively $\left(\text{i.e. } k_t = K_t - \overline{K},\ n_t = N_t - \overline{N}\right)$ and using the identity $\left[1 - \overline{K} / \left(\overline{K} + k_t\right)\right] = \left[k_t / \left(\overline{K} + k_t\right)\right]$, gives an expression for the deviation from the deterministic equilibrium in the full model

$$n_{t+1} = \left[1 - r\left(\frac{\overline{K}}{\overline{K} + k_t} \right) \right] n_t + r\left(\frac{\overline{K}}{\overline{K} + k_t} \right) k_t + r\left(\frac{k_t - n_t}{\overline{K} + k_t} \right) n_t \qquad [5.43]$$

For n_t and k_t small, $\overline{K} / \left(\overline{K} + k_t\right) \approx 1$, and the final term in [5.43] will be negligible. Thus the full non linear model [5.43] should be approximated by the linear model

$$n_{t+1} = (1 - r) n_t + r k_t \qquad [5.44]$$

Following Roughgarden, attention is restricted here to cases where $0 < r < 2$. This corresponds to stability in the deterministic model (i.e. where $K_t = K$).

Local approximation of the moments of the population distribution

Roughgarden investigates in particular the case where k_t is a first order autoregressive process:

$$k_t = \lambda k_{t-1} + Z_t \qquad \left(-1 < \lambda < 1\right) \qquad [5.45]$$

Here Z_t is an independent and identically distributed random variable with zero mean and variance σ_Z^2. Then the variance in the carrying capacity, σ_k^2, is given by

$$\sigma_k^2 = \frac{\sigma_Z^2}{1 - \lambda^2} \qquad [5.46]$$

and the variance in population size in the linear model is then given by

$$\sigma_n^2 = \frac{r}{2-r}\frac{1+(1-r)\lambda}{1-(1-r)\lambda}\sigma_k^2 \tag{5.47}$$

Roughgarden (1975) considers only the case where the equlibrium of the deterministic model is used to estimate the mean population size in the stochastic model. Thus, the mean deviation, $\overline{n}$, is estimated to be zero. In cases where the variation in the carrying capacity is serially independent (i.e. λ in [5.45] is zero) this "first approximation" can also be improved using locally linear approximations (Bartlett 1957, Nisbet & Gurney 1982, p.189, Ellner 1985). Putting $\Delta N_{t+1} = N_{t+1} - N_t$ and $K_t = \overline{K} + k_t$, [5.42] can be written

$$\Delta N_{t+1} = rN_t\left(1 - \frac{N_t}{\overline{K}\left(1 + k_t/\overline{K}\right)}\right) \tag{5.48}$$

Expanding $1/\left(1+k_t/\overline{K}\right)$ in a Taylor series allows [5.48] to be written as

$$\Delta N_{t+1} = rN_t\left(1-\frac{N_t}{\overline{K}}\right) + r\left(\frac{N_t}{\overline{K}}\right)^2 k_t - (\text{other terms}) \tag{5.49}$$

Substituting $N_t = \overline{N} + n_t$ leads to

$$\Delta n_{t+1} = -rn_t - \frac{rn_t^2}{\overline{K}} + \frac{rk_t\left(\overline{N}+n_t\right)^2}{\overline{K}^2} \tag{5.50}$$

Taking expectations in [5.50], and noting that $E(\Delta n) = 0, E\big(f(N)k\big) = 0$ (as only cases where λ is zero are being considered here), and $\sigma_n^2 = E\left(n^2\right) - E(n)^2$ leads to a quadratic expression for the mean deviation:

$$E(n) = \frac{-1}{\overline{K}}\left(\sigma_n^2 + E(n)^2\right) \tag{5.51}$$

where σ_n^2 can be provided by using the linear estimate [5.47] above. The appropriate root of [5.51] is

$$E(n) = \frac{\left(-1+\sqrt{1-4\sigma_n^2/\overline{K}}\right)\overline{K}}{2} \tag{5.52}$$

Roughgarden used a single run of 1000 random numbers to compare the non-linear and full models. Here, prior to investigating the persistence time distribution, a more extensive simulation investigation has been carried out to test the use of the linear approximations in estimating the moments of the full model, as r, λ, and σ_k^2 are varied. Fig. 5.15 demonstrates that the mean value of n_t in the full model is generally less than zero: when λ equals zero the approximate mean deviation given by [5.52] improves upon the assumption that the mean population size in the stochastic model is equal to the deterministic equlibrium. The difference between the numerical estimate of $\bar{n}$ and the prediction of the linear model increases as the variance in carrying capacity increases, and as r is increased.

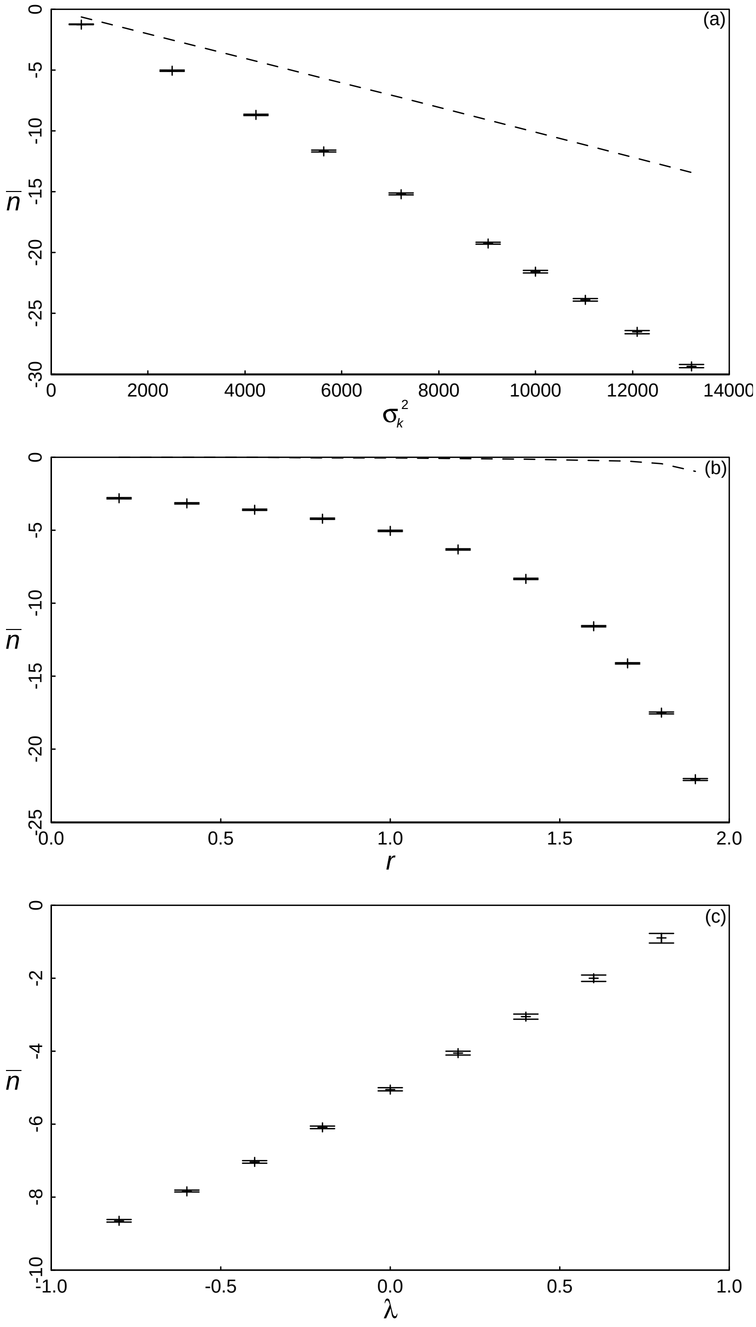


Figure 5.15. Comparison of the mean deviation from the deterministic equilibrium estimated by simulation of the full model [5.43] (points) with the approximation [5.52] (dashed line). Each point is the result of 5000 simulations, each of 1000 time steps. Error bars show 95% confidence intervals. (a) $r = 1$, $\bar{K} = 1000$, $\lambda = 0$; (b) $\bar{K} = 1000$, $\lambda = 0$, $\sigma_k = 50$; (c) $r = 1$, $\bar{K} = 1000$, $\sigma_k = 50$.

Lower values of λ also reduce the mean of n_t in the full model. The fact that the mean of n_t is lower in the full model than either of the approximations to the mean from the linear model is likely to have consequences for the reliability of estimates of the persistence time distribution based on the linear model. The reduction in the mean deviation caused by the non-linearities gives the full model a "push" in the direction of the lower threshold that the linear model does not share.

The variance in n_t for the full model is compared with that given by [5.47] for the linear model in Fig. 5.16. As the variance in carrying capacity is increased the linear model has a tendency to underestimate the variance of the full model. However for higher values of r, the linear model overestimates the full model variance in n_t. For λ in the range -1 to 1 the variance in n_t of the full model is humped (Fig 5.16c) compared with the constant variance predicted by the linear model. However the deviations in Var(n_t) for the full model at different values of λ are small compared to the deviations at higher values of r or σ_k^2. It is thus safe to conclude that for smaller values of r and σ_k^2 the variance given by [5.47] for the linear model is a good approximation of the variance of the full non linear model.

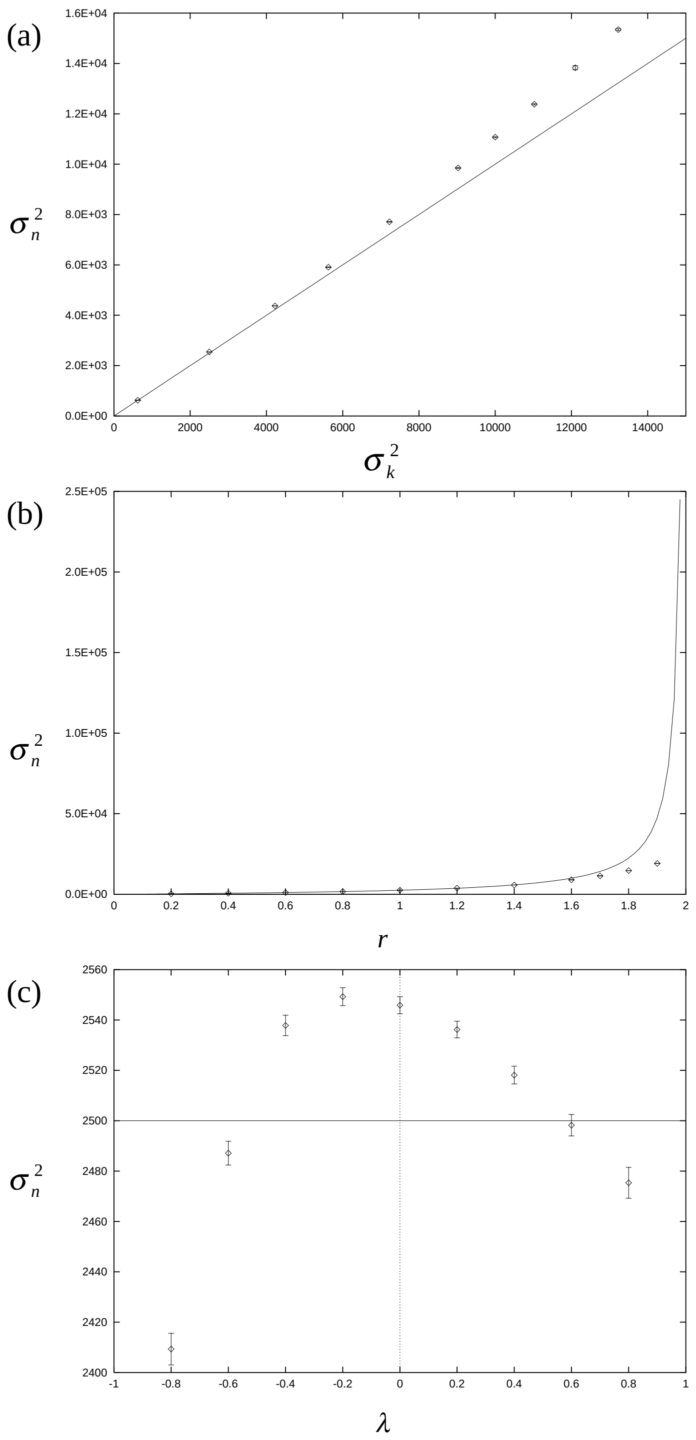


Figure 5.16. Comparison of the variance around the deterministic equilibrium predicted by the linear model [5.44] (line) with the mean deviation estimated by simulation of the full model [5.43] (points). Each point is the result of 5000 simulations, each of 1000 time steps. Error bars show 95% confidence intervals. (a) $r = 1$, $\bar{K} = 1000$, $\lambda = 0$; (b) $\bar{K} = 1000$, $\lambda = 0$, $\sigma_k = 50$; (c) $r = 1$, $\bar{K} = 1000$, $\sigma_k = 50$.

Persistence time distributions

Figs. 5.17 to 5.19 compare the persistence time distributions of Roughgarden's full [5.43] and linear [5.44] models for various sets of parameters, and different values of the lower threshold. To incorporate the linear estimate of the mean deviation from the deterministic equilibrium in Fig. 5.18 (as λ is zero in this case) a second linear model is used :

$$n_{t+1} = (1-r)(n_t - \overline{n}) + rk_t + \overline{n} \qquad [5.53]$$

where $\overline{n}$ is given by [5.52]. For shorter times, the probability of reaching the lower threshold at a time t, $g(t)$, is consistently smaller for both linear models (the persistence time distributions of model [5.53] are slightly nearer the full model persistence time distributions as it takes some account of the fact that the mean population size in the stochastic model is generally less than the deterministic equlibrium). At longer times the distributions tend to cross over giving a higher $g(t)$ for the linear models. However, while the values of the persistence time distributions for the full and linear models are different, the shape of the distributions are broadly similar. In particular, the position of the mode is about the same and, where the full model tends to show a bimodal distribution (e.g. Fig. 5.17b), this feature is also shown by the linear model persistence time distributions. The differences between the linear and full model persistence time distributions in Figs. 5.17 to 5.19 are consistent with the relationships of Figs 5.15 & 5.16. The linear and full model distributions in Fig. 5.17 are closer than those in Fig. 5.18 - this is in line with a slightly decreased mean(n_t) and slightly increased Var(n_t) caused by reducing λ from 0.5 to 0. The rather poor match between the full and linear passage time distributions in Fig. 5.19 can likewise be attributed to the fact that increasing σ_k to 150 means that both linear models significantly overestimate the mean, and underestimate the variance, of the full model's n_t.

Various statistics can be calculated for the numerically estimated persistence time distributions. If T is the last time for which the distribution was estimated, then the total proportion of trials reaching the barrier by time T, $G(T)$, is given by

$$G(T) = \sum_{t=1}^{T} g(t) \qquad [5.54]$$

and the mean persistence time, conditional on reaching the threshold, by

$$E_C(T) = \sum_{i=1}^{T} \left[tg(t) / G(T) \right] \qquad [5.55]$$

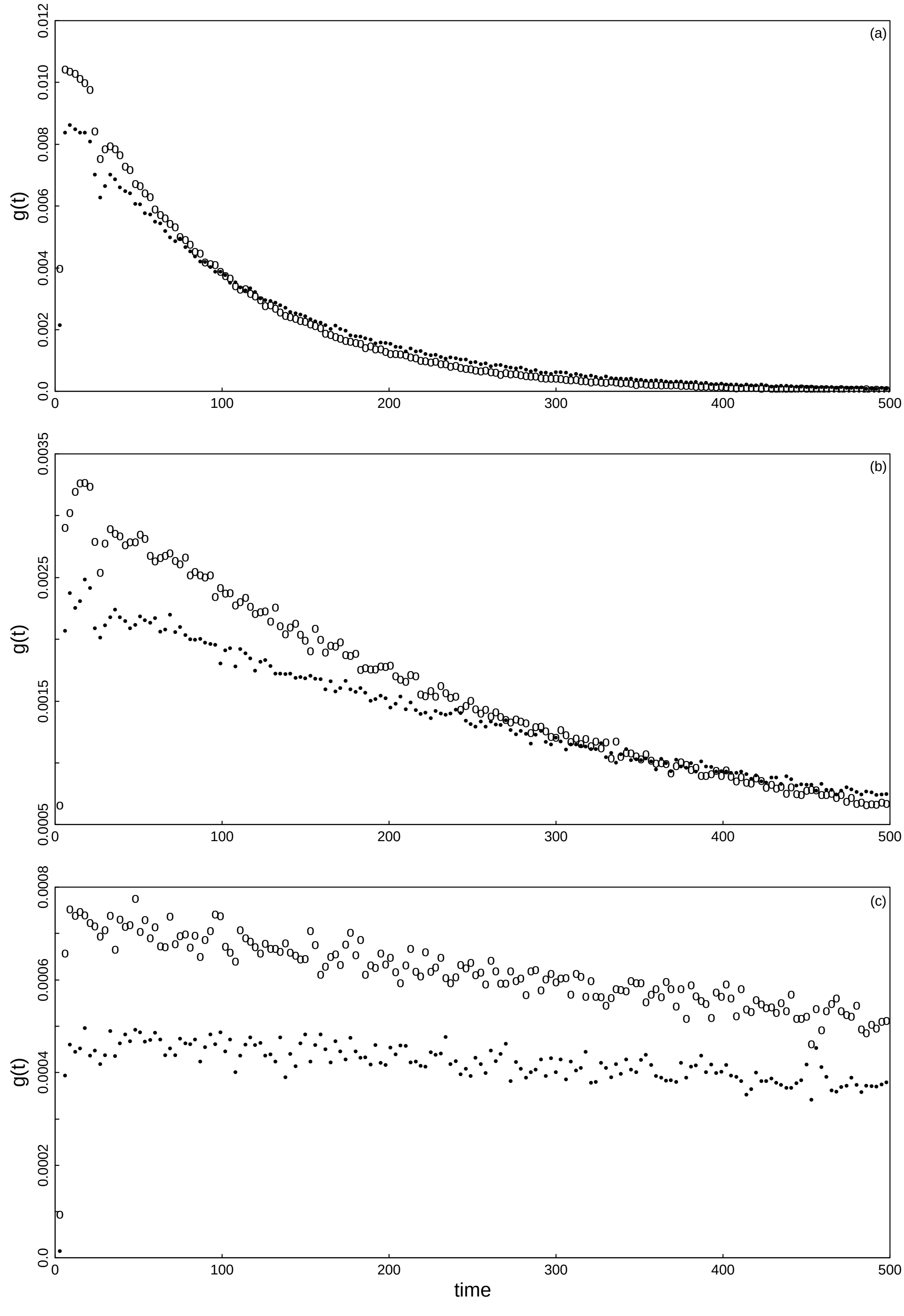


Figure 5.17. Comparison of numerical estimates of the persistence distributions for Roughgarden's full (○) and linear (•) models; $r = 0.5$, $\bar{K} = 1000$, $\sigma_k = 50$, $\lambda = 0.5$, $n_0 = 0$, $k_0 = 20$. Lower barriers at (a) –80, (b) –100, (c) –120.

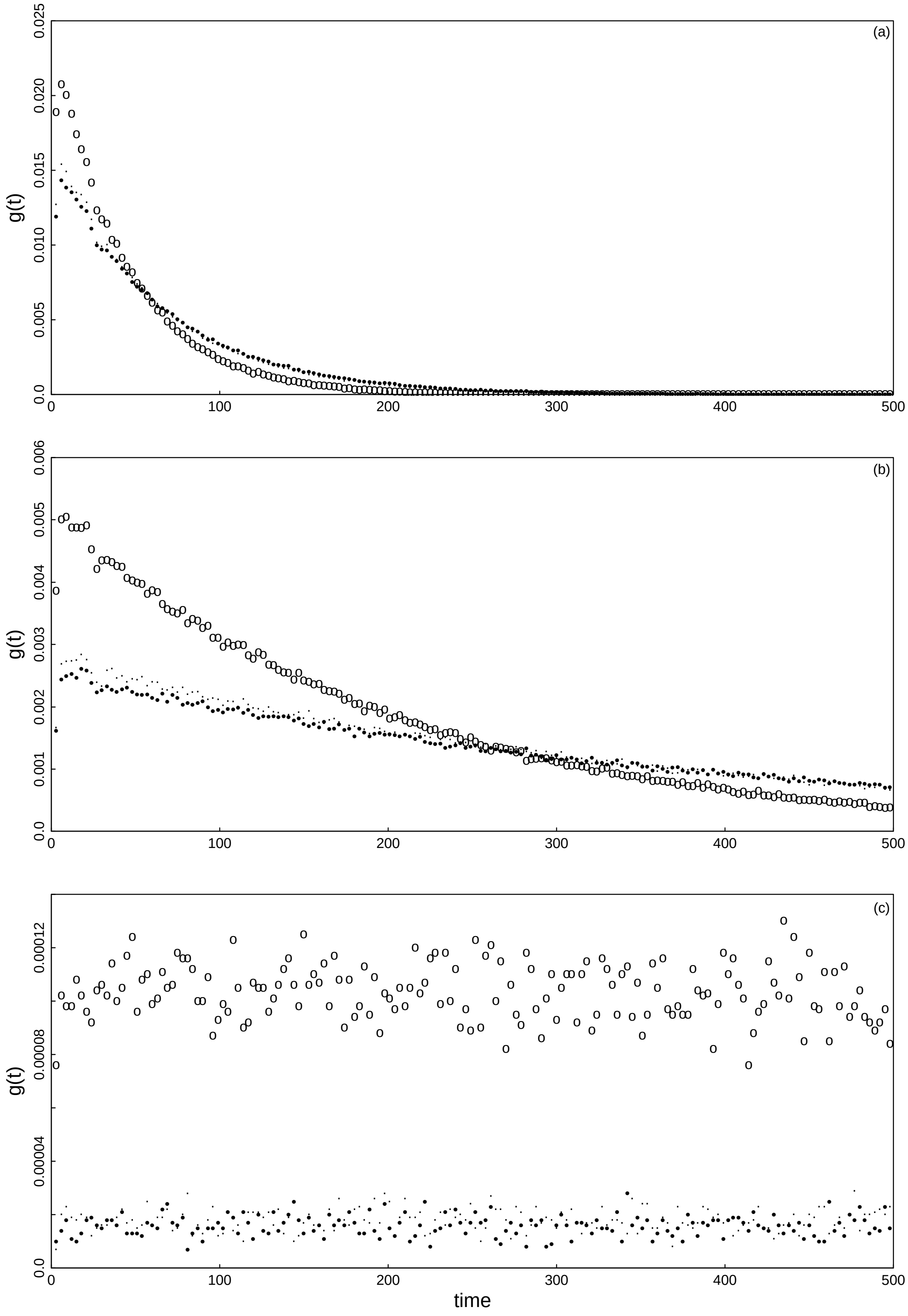


Figure 5.18. Comparison of numerical estimates of the persistence distributions for Roughgarden's full (○) and linear (•) models, and the linear model [5.53] (·); $r = 0.5$, $\bar{K} = 1000$, $\sigma_k = 50$, $\lambda = 0$, $n_0 = 0$, $k_0 = 20$. Lower barriers at (a) –60, (b) –80, (c) –120.

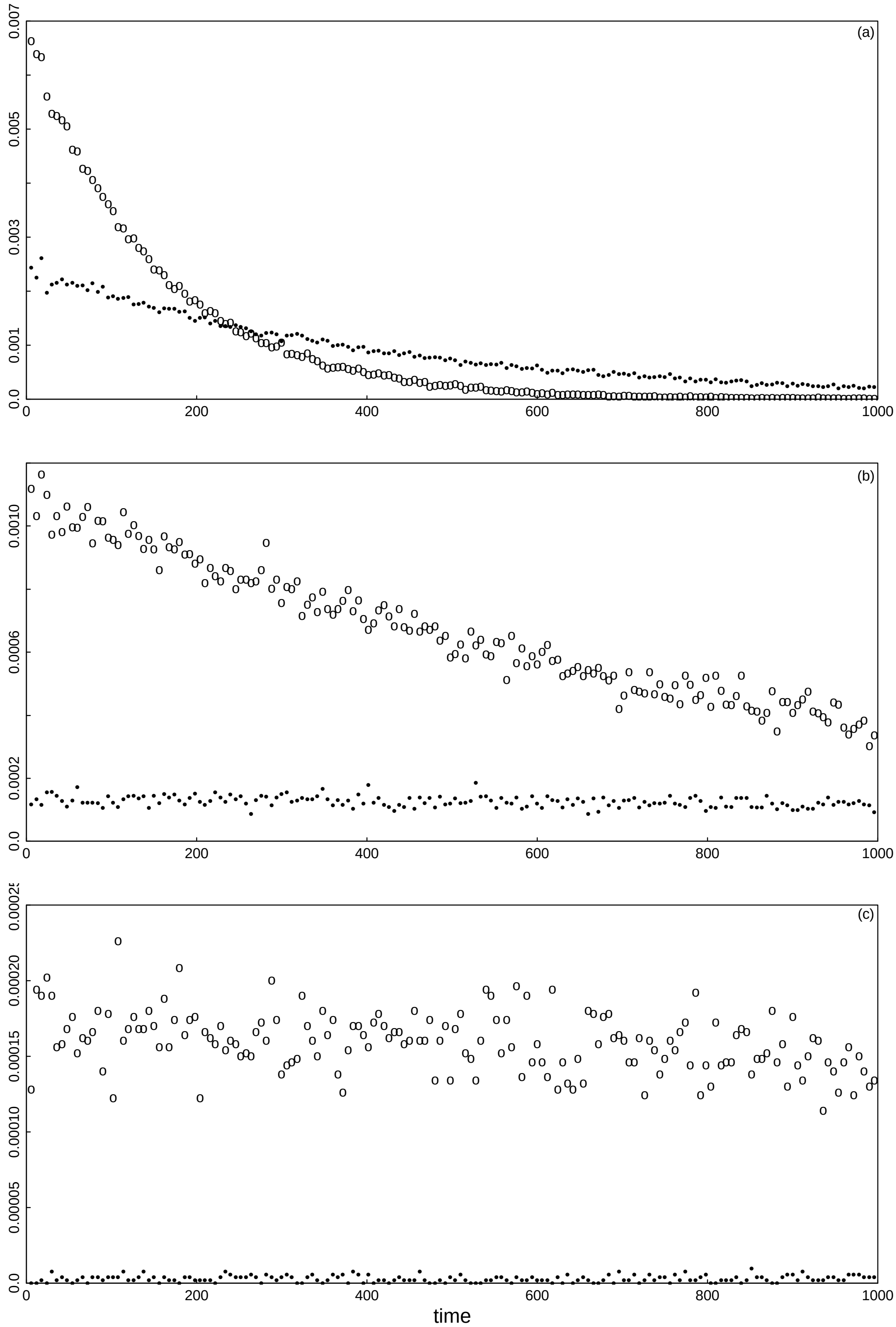


Figure 5.19. Comparison of numerical estimates of the persistence distributions for Roughgarden's full (○) and linear (•) models; $r = 0.5$, $\bar{K} = 1000$, $\sigma_k = 150$, $\lambda = 0.5$, $n_0 = 0$, $k_0 = 20$. Lower barriers at (a) –300, (b) –400, (c) –500.

Table 5.2 shows these statistics, and the mode, for the distributions of Figs. 5.17 to 5.19. Considering first the probability of reaching the threshold by time *T*, it is apparent that as the lower barrier is moved further from the mean population size the difference between $G(T)$ for the full and the linear models increases. $G(T)$ is, in general, larger for the full model, and for lower barriers can be several times larger, than the linear model's $G(T)$. This is in line with the observation that $g(t)$ is generally lower for the linear model than the full model for the times for which the persistence time distribution was calculated. For those cases where a reasonable number of the trials in the simulation reached the threshold the mode of the linear and full distributions are similar. In the cases where the low threshold resulted in few trials being absorbed (i.e. (c) in Figs. 5.17 to 5.19) the mode is highly variable. This is due to the fact that the distributions are very noisy and the position of the mode cannot really be measured with any great accuracy. Comparing the conditional mean of the linear and full, non linear, persistence time distributions gives some encouragement to the idea of using the linear model to estimate the persistence time distribution. In general the two models give similar conditional means, with the linear model consistently giving a slightly longer mean.

Table 5.2. Statistics of the persistence distributions plotted in Figs 5.17 to 5.19. $\bar{K}$ = 1000 in all cases. To remove some of the noise in the distributions and thus facilitate estimation of the position of the mode in the numerically estimated distributions, the distributions were smoothed using symmetric nearest neighbour linear least squares smoothing with a span of 1% of the data range before calculating the statistics given. The conditional mean persistence was also estimated from the smoothed distribution.

	Parameters				mode		$E_C(T)$		$G(T)$	
	r	σ_k	λ	n_a	full	linear	full	linear	full	linear
Fig. 5.17a	0.5	50	0.5	−80	9	10	91.5839	108.608	0.991	0.985
Fig. 5.17b	0.5	50	0.5	−100	18	18	188.91	205.198	0.799	0.696
Fig. 5.17c	0.5	50	0.5	−120	17	14	237.752	243.102	0.305	0.209
Fig. 5.18a	0.5	50	0	−60	7	7	45.6402	67.2682	0.994	0.995
Fig. 5.18b	0.5	50	0	−80	9	19	155.55	200.996	0.921	0.716
Fig. 5.18c	0.5	50	0	−120	106	69	249.17	252.914	0.051	0.007
Fig. 5.19a	0.5	150	0.5	−300	10	15	151.461	321.377	0.996	0.907
Fig. 5.19b	0.5	150	0.5	−400	19	190	413.366	492.562	0.664	0.126
Fig. 5.19c	0.5	150	0.5	−500	111	231	487.858	495.361	0.160	0.003

Approximating the linear model passage time distribution using the OU process

The results of the previous section demonstrate that the linear model persistence time distribution, while certainly not reproducing the distribution of the full model, can at least give some insight into the full model's distribution. In particular the conditional mean persistence time of the linear model can be a reasonable estimate of that of the full model.

In this section, therefore, the approximation of the linear model by the Ornstein-Uhlenbeck process (for which an expression for the mean first passage time is given in chapter 2) is investigated.

Renshaw (1987) discusses a discrete time analogue for the OU process. The result of interest here is that, for an OU process as given by Uhlenbeck & Ornstein (1930):

$$m\frac{dU}{dt} = -fU + F(t) \qquad [5.56]$$

where $F(t)$ is white noise, the equivalent discrete scheme is

$$U_t = U_{t-1}(1-\delta) + \varepsilon_t \qquad [5.57]$$

where $\delta = f/m$, and $\varepsilon_{t+1} = (1/m)F_n$. For independent and identically distributed ε_t [5.57] is, of course, a first order autoregressive process.

When $\lambda = 0$ in [5.45] (i.e. the fluctuations in the carrying capacity are generated by an independent, identically distributed process rather than an autoregressive process) Roughgarden's linear model [5.44] also yields an autoregressive process of order one:

$$n_{t+1} = (1-r)n_t + r\sigma_k Z_t \qquad [5.58]$$

Using Renshaw's result above, Cerbone, Ricciardi & Sacerdote's formula for the mean first passage time of the OU process, as given in [2.50], can be applied:

$$\begin{aligned} E(T) = \frac{1}{r}\Bigg[& \frac{1}{2}\left(\psi\left[-n_a\left(\frac{(r\sigma_k)^2}{2r}\right)^{-\frac{1}{2}}\right] - \psi\left[-n_0\left(\frac{(r\sigma_k)^2}{2r}\right)^{-\frac{1}{2}}\right]\right) \\ & + \left(\frac{\pi}{2}\right)^{\frac{1}{2}}\left(\chi\left[-n_0\left(\frac{(r\sigma_k)^2}{2r}\right)^{-\frac{1}{2}}\right] - \chi\left[-n_a\left(\frac{(r\sigma_k)^2}{2r}\right)^{-\frac{1}{2}}\right]\right)\Bigg] \end{aligned} \qquad [5\ .59]$$

where n_a represents the threshold level and $\psi[z]$ and $\chi[z]$ are given in [2.51].

To test this, Table 5.3 compares the expected persistence time calculated from [5.59] with that estimated from numerical distributions using [5.55].

Estimating the expected persistence time from simulated distributions using eqn [5.55] requires that the complete distribution be estimated in order to obtain a reliable estimate of the expectation. Another approach is however possible. As the distribution of persistence times being considered is believed to be asymptotically exponential then the tail of the distribution should be linear when plotted semi-logarithmically ($\ln[g(t)]$ vs. t). From the equation of the line the coefficient of the exponential distribution can then be recovered. This coefficient is the expected persistence time from a zero initial state to the lower threshold. Specifically, given a "one-parameter" exponential distribution (Johnson & Kotz 1970):

Table 5.3. Expected persistence times for Roughgarden's linear model [5.44] from [5.59] and from [5.55] for numerical estimates of the passage time distribution. In order that [5.55] would yield a figure suitable for comparison with [5.59] it is necessary that the whole passage time distribution be calculated i.e. the numerically estimated passage time distribution must have maximum time, T, such that $g(t) = 0$ for all $t > T$. The parameters used here are chosen so this criteria can be fulfilled.

Parameters				$E_C(T)$	
r	σ_k	n_0	n_a	formula	simulation
0.5	50	0	−60	43.989	67.1631
1	50	0	−60	6.300	9.698
1.5	50	0	−60	2.575	4.656
0.5	75	0	−60	10.798	18.285
0.5	100	0	−60	5.780	10.958
0.5	125	0	−60	3.916	8.348
0.5	150	0	−60	2.956	7.041
0.5	50	5	−80	297.904	396.135
1	50	5	−80	16.641	19.212
1.5	50	5	−80	5.276	6.301
0.5	75	5	−80	26.108	41.367
0.5	100	5	−80	10.557	18.280
0.5	125	5	−80	6.359	12.052

$$g(t) = \frac{1}{E_0(T)} \exp\left(\frac{-t}{E_0(T)} \right) \qquad [5.60]$$

where $g(t)$ is the asymptotic persistence distribution and $E_0(T)$ is the expected passage time from zero to the threshold then

$$\ln[g(t)] = \ln\left[\frac{1}{E_0(T)} \right] - \frac{t}{E_0(T)} \qquad [5.61]$$

By comparison with the equation of a straight line, $y = ax + b$, $E_0(T)$ can be estimated from either the intercept of the line $\ln[g(t)]$ vs. t, $E_0(T) = -1/a$, or its slope, $E_0(T) = 1/\exp(b)$. Fig 5.20 shows that plotting $\ln[g(t)]$ vs. t for Roughgarden's linear model does indeed yield a linear relationship. Two lines have been fitted to the points of Fig 5.20, one using normal least squares regression, the other using more robust (Rousseeuw & Leroy 1987) least median squares regression. Clearly the least median squares line is going to give a better indication of the slope, and this has therefore been used whenever $E_0(T)$ has been estimated from the simulated passage

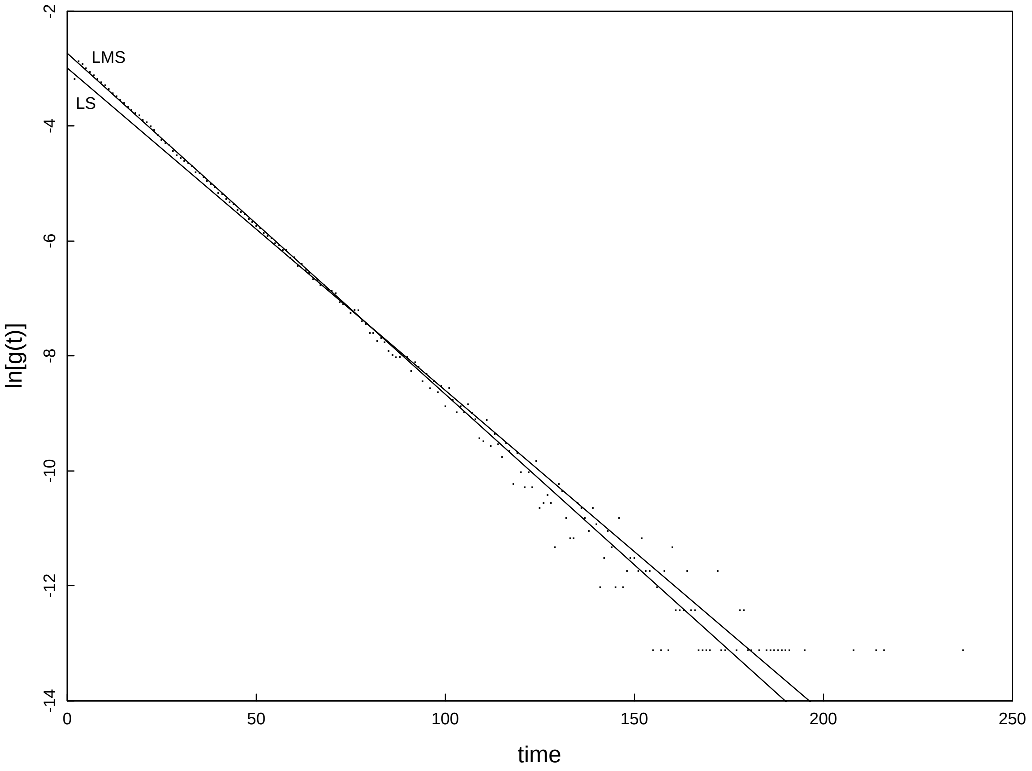


Figure 5.20. Plot of $\ln[g(t)]$ vs. t for Roughgarden's linear model [5.44] with $r = 0.5$, $\sigma_k = 75$, $n_0 = 0$, $n_a = -60$. The lines are fitted by least squares regression (LS) and least median squares regression (LMS).

time distributions.

Table 5.4 compares the values of $E_0(T)$ recovered by fitting a straight line to $\ln[g(t)]$ vs. t, with the value given by [5.55] for the same simulated distributions as Table 5.2, and the discrete OU approximation [5.59]. The three estimates of $E_0(T)$ from the simulated distributions generally agree to within ±5, and are such that the estimation from the intercept of the straight line is less that the estimate from the slope, which in turn is less the estimate from eqn. [5.59]. All three estimates however share the feature, also apparent in Table 5.3, that the discrete OU approximation generally

Table 5.4. The expected persistence from a zero initial state to a lower threshold for Roughgarden's linear model. OU approx. gives the approximate persistence time from [5.59]. The remaining columns give estimated derived from the simulated distributions used in Table 5.2. 'estimate' refers to the estimate from [5.55] (and is therefore not available for simulated distributions where not all replicates reached the lower threshold by the last time considered), 'intercept' and 'slope' refer to the estimates derived from fitting a straight line to $\ln[g(t)]$ vs. t. Least median squares regression was used and, before the regression was carried out, values falling to the left of the mode of the distribution were removed so regression was only carried out on the linear portion of the data (i.e. the exponential tail of the distributions).

Parameters			$E_0(T)$			
r	σ_k	n_a	OU approx.	estimate	intercept	slope
0.5	50	−60	43.989	67.1631	62.90	65.37
1	50	−60	6.300	9.698	7.18	8.33
1.5	50	−60	2.575	4.656	1.95	3.14
0.5	75	−60	10.798	18.285	15.33	16.84
0.5	100	−60	5.780	10.958	8.64	9.67
0.5	125	−60	3.916	8.348	6.04	7.08
0.5	150	−60	2.956	7.041	4.87	5.86
0.5	50	−80	298.37		393.66	396.05
1	50	−80	16.81		16.52	17.79
1.5	50	−80	5.37		3.12	4.61
0.5	75	−80	26.43		37.29	39.24
0.5	100	−80	10.80		14.88	16.54
0.5	125	−80	6.55		9.57	10.70

underestimates the actual expected persistence. In a few cases (notably those with $E_0(T)$ small) the discrete OU approximation yields a value of $E_0(T)$ which actually falls within the estimates from the simulated passage time distribution, but overall the result is rather disappointing.

The explanation for this appears to associated with using results for the continuous time OU process for a discrete time model. In chapter 3 it was noted that the Wiener process did not give an exact fit to persistence time distributions for a discrete time model, in particular it tended to produce a slight overestimate of the probability of reachng the threshold in the region of the mode. In that case, however, the Wiener process still gave reliable estimates for the moments of the persistence time distribution. The same cannot be said for the OU process and the discrete time model considered here. Fig. 5.21 demonstrates that simulating [5.58] with time steps less than one produces a steeper relationship between the linear portion of ln[$g(t)$] and time. While this steepening appears relatively slight, it is apparent from [5.61]

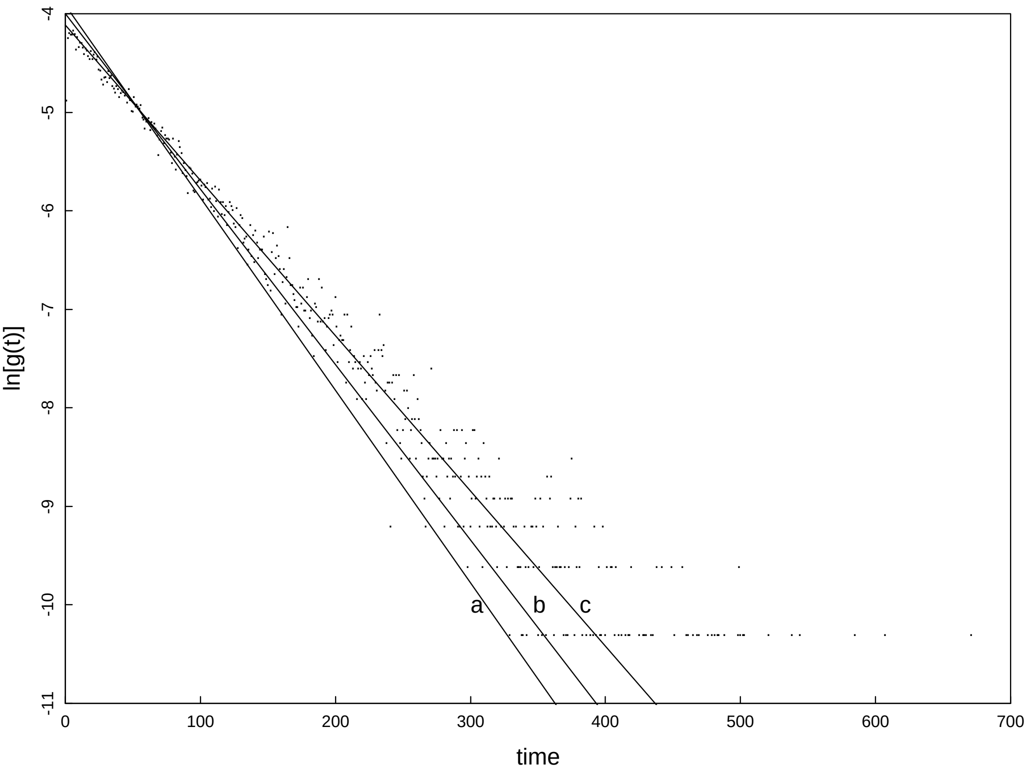


Figure 5.21. The log probability of reaching the threshold for the linear model [5.58]. $n_0 = 0$, $n_a = -60$, $r = 0.5$, $\sigma_k = 50$. Line c is fitted to the points (by least median squares regression) for a simulation with $\Delta t = 1$. Lines a and b are fitted to simulations with $\Delta t = 0.01$ and 0.1 respectively.

that a smaller time step results in a smaller estimate of mean persistence time. Thus, as Δt is reduced the mean first passage time for the OU process provides a better estimate of persistence time for "discrete OU" models.

Exponential approximation of the persistence time distribution

So far in this section Nobile, Ricciardi & Sacerdote's (1985) results have been used exclusively to estimate the mean persistence time for the linear model. As discussed in chapter 2, and applied above, it is possible to approximate the persistence time distribution simply as an exponential distribution. This is done in Fig 5.22, which uses the same simulated persistence time distributions as Fig 5.18. Two one-parameter exponential curves have been added to each plot, one with the coefficient estimated by fitting the tail of the linear model persistence time distribution as described above, the other by using the mean OU persistence time from zero to the threshold as the coefficient. The simple exponential distribution, with the coefficient obtained by least mean squares regression on the distribution tail, gives a very good approximation of the persistence time distribution for the linear model with the exception of very short times.

In Fig. 5.23 $\ln[g(t)]$ vs. t for Roughgarden's full model is plotted. The distributions clearly have a linear tail demonstrating that the full non-linear model gives rise to an asymptotically exponential persistence time distribution. What is yet to be obtained is, of course, an analytical approximation for the mean persistence time that performs better than the linear approximation considered above.

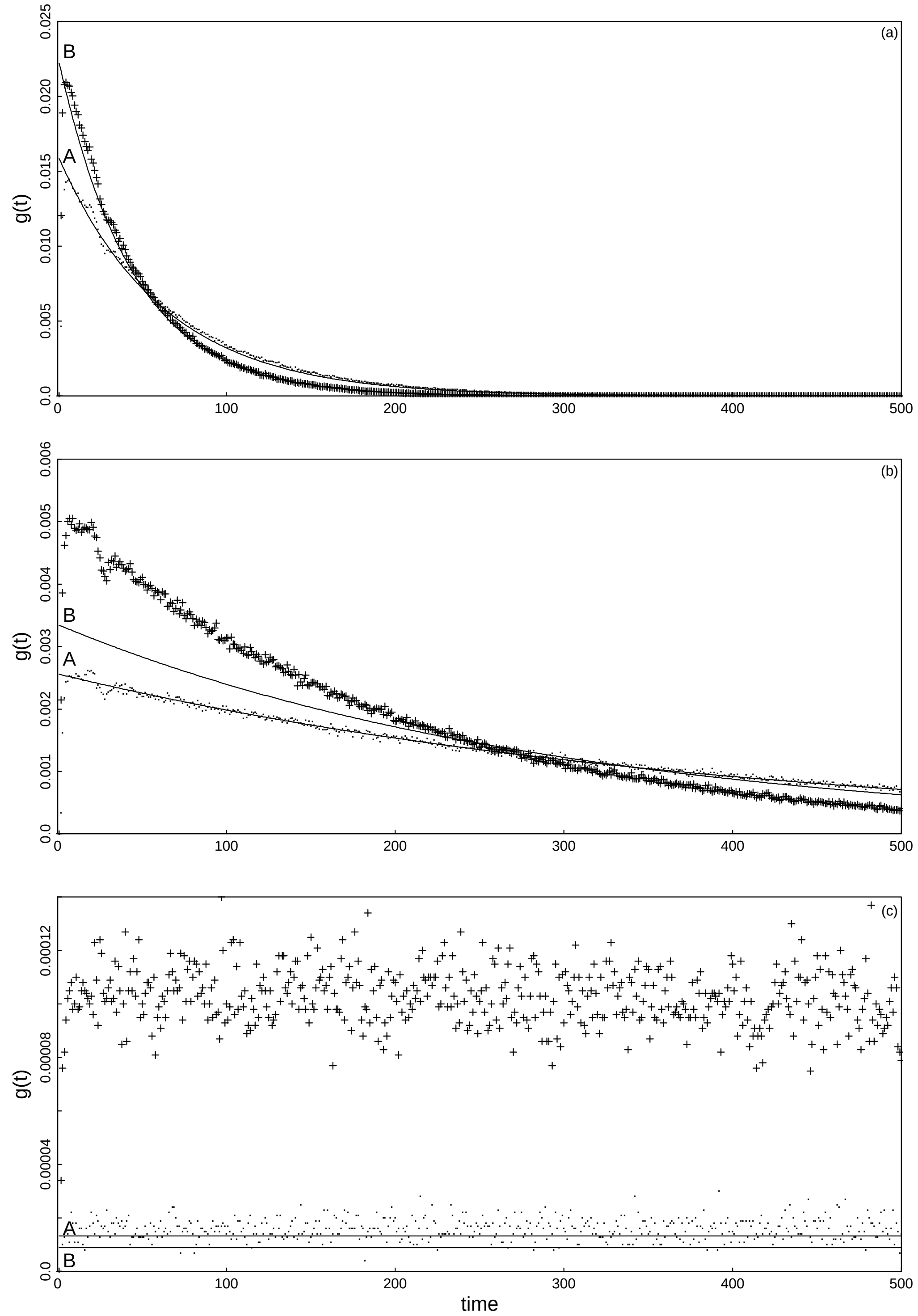


Figure 5.22. Comparison of numerical estimates of the persistence distributions for Roughgarden's full (+) and linear (·) models; $r = 0.5$, $\bar{K} = 1000$, $\sigma_k = 50$, $\lambda = 0.5$. $n_0 = 0$, $k_0 = 20$. Lower barriers at (a) −80, (b) −100, (c) −120. Exponential curves added using coefficient estimated from (A) slope of a least median squares regression for the linear portion of $\ln[g(t)]$ vs. t of the linear model, (B) mean persistence from zero to threshold as given by OU approximation [5.59].

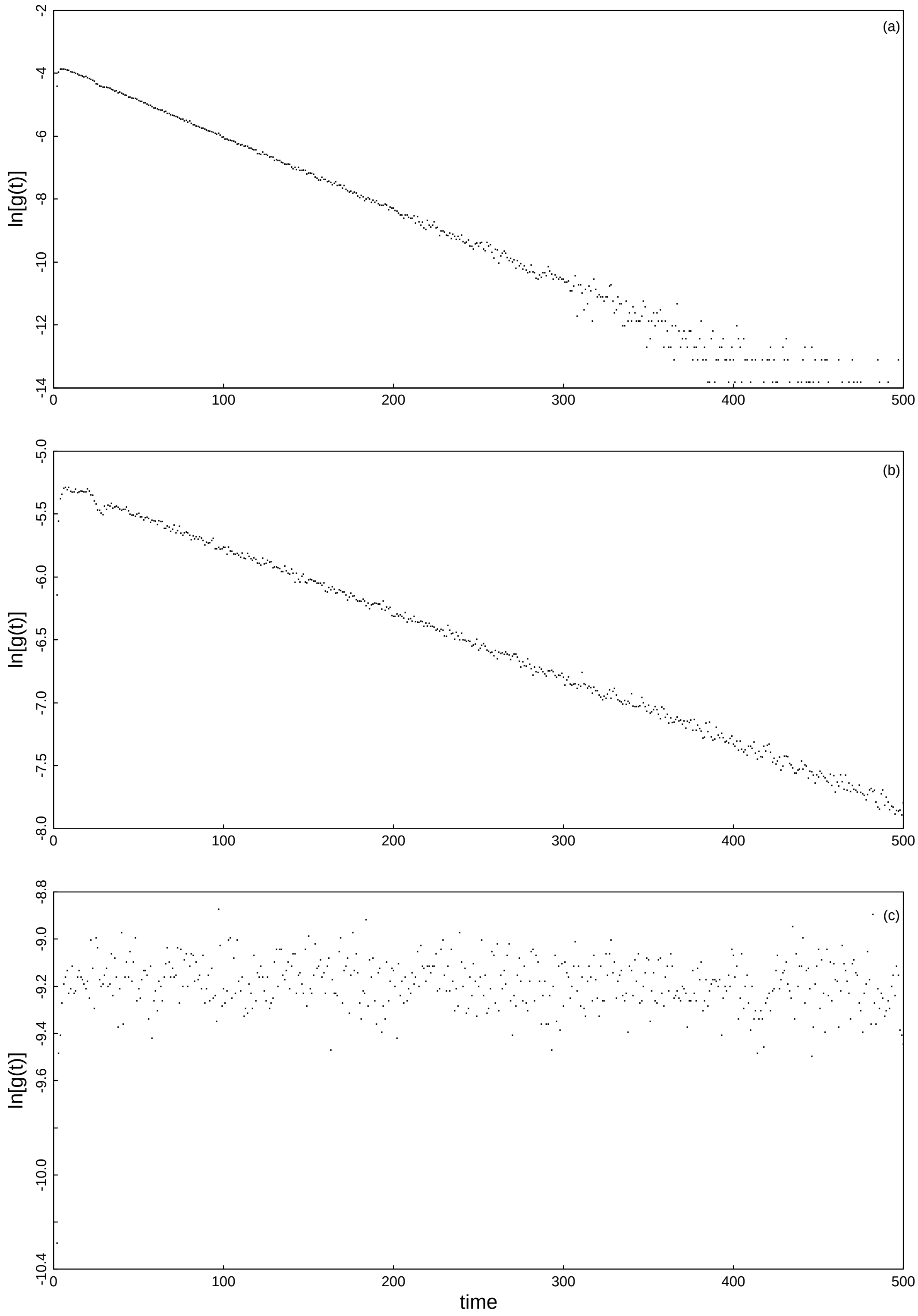


Figure 5.23. ln[$g(t)$] vs. t for Roughgarden's full model; $r = 0.5$, $\bar{K} = 1000$, $\sigma_k = 50$, $\lambda = 0.5$. $n_0 = 0$, $k_0 = 20$. Lower barriers at (a) –80, (b) –100, (c) –120.

Discussion

In this section two things have been investigated. Firstly, a numerical comparison of persistence times in a non-linear population model and a simpler model obtained by local linearisation of the full model, was carried out. Secondly, the approximation of the persistence time distribution of locally linear model (a first order autoregressive process) by the first passage time distribution of the OU process was considered.

It is apparent, from the results obtained above, that there can be quite large differences between the persistence time distributions of the full non-linear model, and its linear counterpart. In general, the full model shows a greater probability of reaching a low threshold at short or intermediate times, than the linear model. These differences are explained by recourse to the differences between the mean and variances of the full model [5.43] and the linear model [5.44] investigated initially. In particular the mean population size of the non-linear model is always smaller than that of the linear model. In addition, as the variance in the carrying capacity is increased, the variance in population size in the non-linear model is underestimated by the variance in the linear model.

Two features, however, suggest that locally linear approximations may be of some use in the estimation of persistence time in non-linear models. Firstly, the shapes of the persistence time distributions of the linear and non-linear models tend to be similar, generally showing a common mode (though, of course, no expression for the mode of the linear model is actually available at present). The similarity in shape leads, however, to the fact that the conditional mean persistence time in the full model and linear model are similar. Understandably the linear model, with its smaller probability of reaching the threshold at small times, has the larger conditional mean. For various sets of parameters the linear and non-linear model conditional mean persistence time have a similar, though not identical, rank order. This suggests that a linear approximation may be of use in giving a qualitative idea of the effect on expected persistence time of changing one of the full model parameters. However, locally linear approximations are unlikely to be of much use in comparing persistence times between different models.

The use of the OU process first passage time distribution to approximate the expected persistence time of the linear model, which took the form of a first order autoregressive process, also produced rather equivocal results. In general, the expected persistence time suggested by the OU process approximation was less than that from numerical estimates of the linear model's persistence time distribution. This appears to be due to the estimation of results for a discrete time model from the continous time OU process: where a continous time model is linearised to produce an OU process this difficulty should not arise. The continuous OU process can give an estimate of persistence time correct to order of magnitude for a discrete model but cannot be expected to be much more accurate.

Both of the linear models considered here ([5.44] and [5.53]), and the OU process itself, share the feature that the state variable is normally distributed around the mean. Nisbet & Gurney (1982, p.207-210) demonstrate that a skewed distribution may be more appropriate. Using locally linear approximations to the mean and variance they show that considering a negative binomial, rather than a normal, distribution improves their estimates of extinction time. Dennis & Patil (1984) suggest using the gamma distribution to approximate the distribution of a stochastic model where the corresponding deterministic model has a stable equilibrium.

One feature shared by persistence time distributions of the full non-linear model and the local linearisation is that the distribution is exponential at all but short times. As discussed previously, this is likely to be a feature of most models where the population size is regulated around some mean value. Features of the persistence time of the continuous time logistic considered previously, such as the rapid increase in mean persistence time as the distance between the mean population size and the lower threshold is increased (Fig. 5.12), will also arise in such situations.

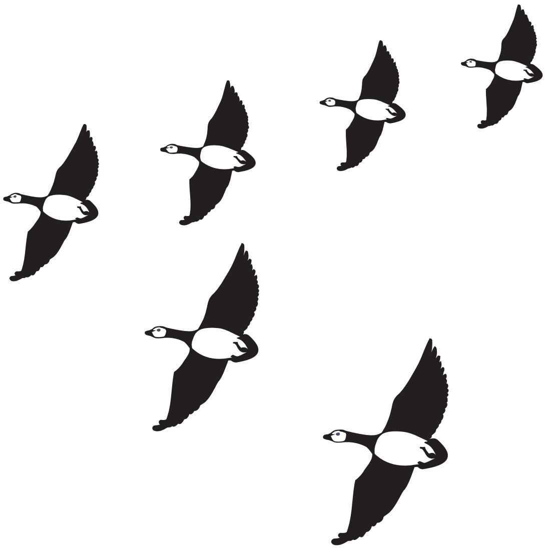
II

Persistence time applied in assessing management of the Islay wintering barnacle geese

This section presents the work that led to my interest in persistence time in population models, and in particular its use as a viability measure in the conservation management of populations.

Chapter 6 presents an overview of the distribution and biology of the barnacle goose. The situation of the wintering geese on Islay that has led to the conflict between agricultural and conservation interests is considered, and the available data analysed.

In chapter 7 persistence time is used as the primary population viability measure in the assessment of controlled shooting as a management strategy, with the aim of discovering whether this method could lessen agricultural problems without endangering the goose population.



Chapter 6

Barnacle geese on Islay: population status and agricultural conflicts

The barnacle goose

World distribution

The barnacle goose, *Branta leucopsis* Bechstein, is a medium sized goose, 58–70cm in length with a wing span of 132–145cm (Cramp & Simmons 1977). Like many western Palearctic goose species (Madsen 1991) its population size has increased greatly in the second half of this century. In 1960's the world population was estimated at 40,000 individuals, growing to c.80–90,000 in 1986 (Owen, Atkinson-Willes & Salmon 1986). Owen (1990b) suggests that the current world population of barnacle geese stands at over 120,000 individuals.

Traditionally the world population has been separated into distinct three sub-populations (Fig. 6.1) (Owen 1980), breeding in east Greenland (c.30,000 birds in 1976), Svalbard (c.7000 birds in 1976) and western Siberia (c.54,000 birds in 1976/77). However, during the 1980's a fourth population of c.5000 individuals became established in Gotland and neighbouring islands of the Swedish Baltic (Owen 1990b). The largest (Siberian breeding) group winters in the Netherlands (Owen, Atkinson-Willes & Salmon 1986), but the Greenland and Svalbard populations winter exclusively in British Isles. The Greenland breeding group winters mainly on islands off western Scotland and Ireland, while the Svalbard population winters on the Solway Firth. Ringing suggests the populations are basically discrete, even in winter when the Greenland and Svalbard populations are separated by less than 150km (Owen 1990b). A small amount of interchange does occur: Owen (1990b) reports that 0.1% of ringed individuals have moved from the Svalbard population to other populations. Percival (1988) found that nine birds, previously marked in the Svalbard population, had been incorporated in the Greenland population and that three of these had bred successfully during the three year period of his study. Only one ringed goose from the Greenland breeding population has been recorded with the Svalbard birds, spending one winter on the Solway but later moving back to the Greenland population (Owen 1990b). As a smaller proportion of the Greenland breeding population are ringed compared to the Svalbard group, immigration from the Greenland breeding group is less likely to be detected.

The fact that such a large part of the world population of barnacle geese winter in a relatively small area of the British Isles appears to have been a major reason for the species inclusion in Annex 1 of the EEC directive on the conservation of wild birds

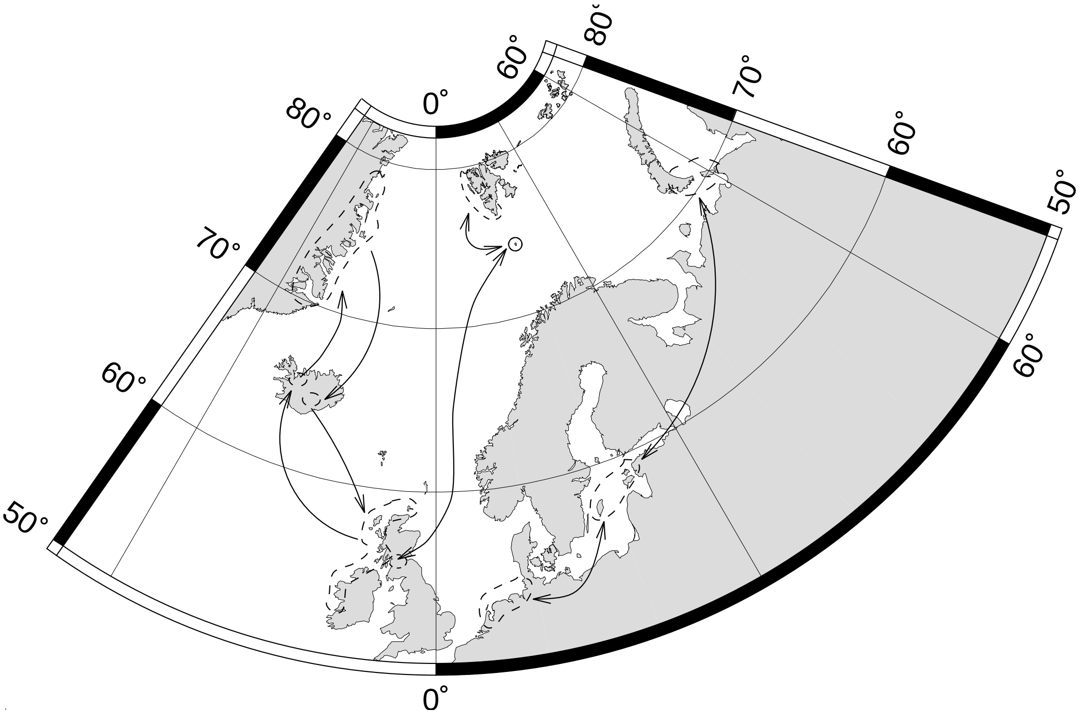


Figure 6.1. The breeding, staging and wintering grounds of the three main world populations of the barnacle goose, *Branta leucopsis*. From information in Owen, Atkinson-Willes & Salmon (1986).

(EEC, 1979). The Annex 1 species are to be the subject of conservation measures relating to their habitat, in order to ensure their "survival and reproduction in their area of distribution". They are also protected from hunting and sale (Haigh 1984). Britain's compliance with this EEC directive is part of the Wildlife and Countryside Act of 1981 (Haigh 1984).

General ecology

Barnacle geese are gregarious throughout the year. They form monogamous, life long pair bonds, but if a bird's mate dies, or is separated during migration, it will form a new pairing (Cramp & Simmons 1977; Owen 1990b). Outside the breeding season flocks include family parties, adults without broods (mostly in pairs) and second year birds, some of which are paired. Barnacle geese may live for up to twenty years (Owen & Black 1989).

Breeding

Barnacle geese arrive on their arctic breeding grounds in late May. They are ready to breed immediately but may be delayed by snow cover for up to two weeks (Owen

1980). Nests are built on rocky cliffs away from Arctic foxes. Cramp & Simmons (1977) state that a pair raises one brood, with a normal clutch size of four to five eggs. Eggs are laid largely from body reserves (Owen & Black 1989) and are incubated by the female for 24 to 25 days. This is followed by a fledging period of 40 to 45 days. The young stay with their parents until they return to breeding grounds in the subsequent year. The usual age of first breeding is three years, but occasionally two.

Breeding success in barnacle geese is highly variable from year to year. On the wintering grounds the three populations have shown proportions of first year birds ranging from 7.5 to 47.2% (Cramp & Simmons 1977). Breeding success depends critically on the condition of the female on arrival on breeding grounds, the greatest loss of breeding potential being due to a failure to nest, or to remain loyal to the nest (Owen 1990b). Losses of goslings during the first week after hatching are high, and by arrival on the wintering grounds the average brood size has decreased from 3.5 – 4 to about 2 (Owen 1990b). Cabot *et al.* (1984) report that 15% of goslings leaving the nest were lost to predators (mainly Arctic foxes) while 26% were lost in the boulder scree at the foot of the cliffs used for nesting. In both the Greenland and Svalbard breeding populations a high proportion of the geese fail to breed each year, such that only a relatively small proportion of the adults on the wintering grounds (up to c.15%) are part of family groups with young (Cabot & West 1983).

Wintering

Losses on autumn migration from the breeding to wintering grounds appear to be the main source of year-to-year mortality in barnacle geese (Owen 1990b). Owen (1990b) suggests that shooting is the main source of overwinter mortality as winter food supplies are largely unlimited, with the only reports of winter starvation in barnacle geese coming from the Outer Hebrides, in severe winters.

On the wintering grounds the geese roost in large groups, no further than 5km from their feeding grounds (Owen, Atkinson-Willes & Salmon 1986). While their traditional habitat is machair (grassland on shell sand) most wintering barnacle geese now feed on agricultural grasslands. Black, Deerenberg & Owen (1991) studied barnacle geese of the Svalbard population on their staging grounds off western Norway. In recent years an increasingly large part of the population has moved to feeding on agricultural grassland in preference to the traditional rougher grazing.

Their observations suggest that conditions are more favourable on the agricultural land with geese feeding at a higher rate, and spending less time in total on feeding, than on the traditional grazing sites. They found some (non significant) evidence that the geese feeding on the agricultural land have higher reproductive success.

The east Greenland breeding population

The east Greenland breeding barnacle geese leave their breeding grounds from mid-September, stopping for a month in southern Iceland before arriving in the British Isles in late October. They remain on the wintering grounds until April, stopping for three weeks in north-western valleys of Iceland on their journey back to the Greenland (Owen, Atkinson-Willes & Salmon 1986) (see Fig. 6.1).

The wintering grounds of the east Greenland barnacle geese are scattered widely over the west coasts of Scotland and Ireland, mostly on islands (Fig. 6.2). The majority of

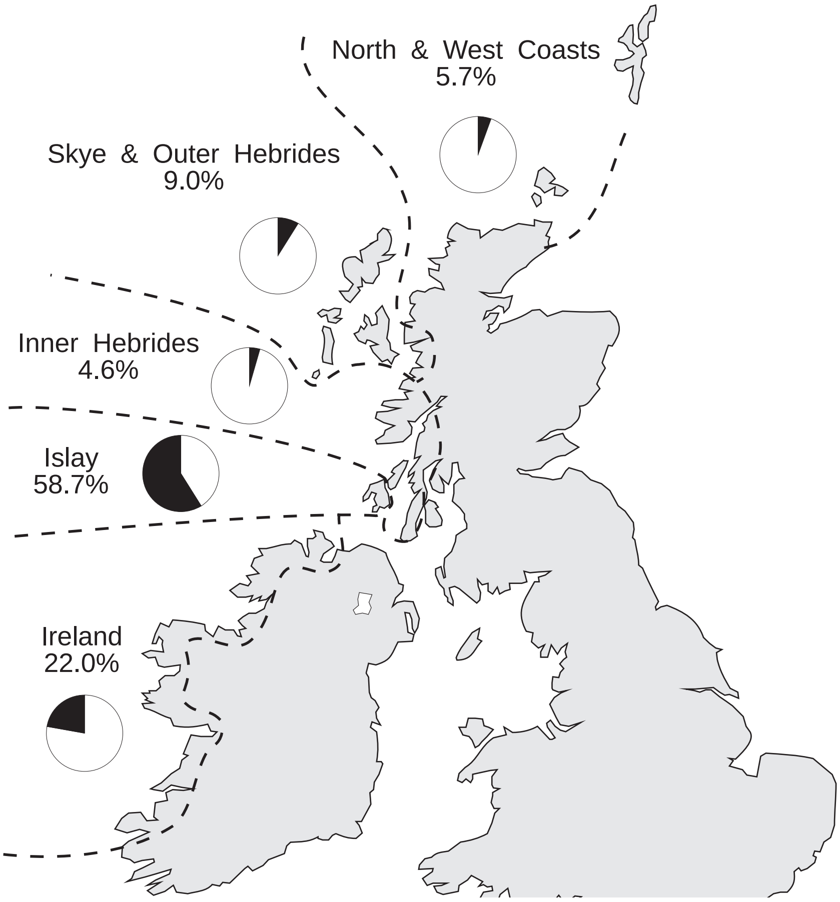


Figure 6.2. The distribution of the east Greenland breeding barnacle goose population on its wintering grounds recorded by the March 1988 aerial survey (Fox *et al.* 1990).

the population, however, winters on Islay in the Inner Hebrides. Islay has held around 60% of the Greenland population since the 1960's.

Counts

No attempts were made to census the wintering Greenland barnacle geese before 1955 due to the dispersed nature of the wintering grounds (Boyd 1968). Numbers prior to this date rely on a mixture of sources of varying reliability. Air censuses are the only way of counting the whole Greenland population, as a large number of islands that make up the wintering grounds are remote and uninhabited (Ogilvie 1983b). However, the numbers of birds on Islay are such that aerial counts would be impractical so the Islay wintering birds have always been counted from the ground. Air censuses have taken place at five year intervals in recent years and are generally carried out in late March or early April (Fox e*t al.* 1990).

Boyd (1968) reports irregular counts of the Islay wintering portion of the east Greenland barnacle geese, made by a number of people, going back to 1952. Regular November and spring (March or April) counts of the Islay wintering geese began in the mid-1960's (Ogilvie 1983a). Counting has intensified in recent years with monthly counts by Nature Conservancy Council (now Scottish Natural Heritage) and Wildfowl and Wetlands Trust personnel (Easterbee *et al.* 1987; Bignal, Curtis & Matthews 1988).

First winter barnacle geese retain juvenile coverts and other juvenile feathers (Cramp & Simmons 1977) enabling the proportion of young in wintering flocks to be estimated. This has been done for the Islay wintering birds in conjunction with the annual counts. Estimates of the proportion of young in the Islay wintering barnacle geese typically involve counting at least 4000 birds (Ogilvie 1983b). There are some problems in the estimation of the proportion of young birds, such as the fact that young geese tend to be concentrated at the edges of feeding flocks (Owen 1980). However, in their work on the Russian breeding population of barnacle geese Ebbinge, van Biezen & van der Voet (1991) found no significant difference between estimates of the proportion of young in a flock from observations compared to the proportion estimated from birds caught for ringing.

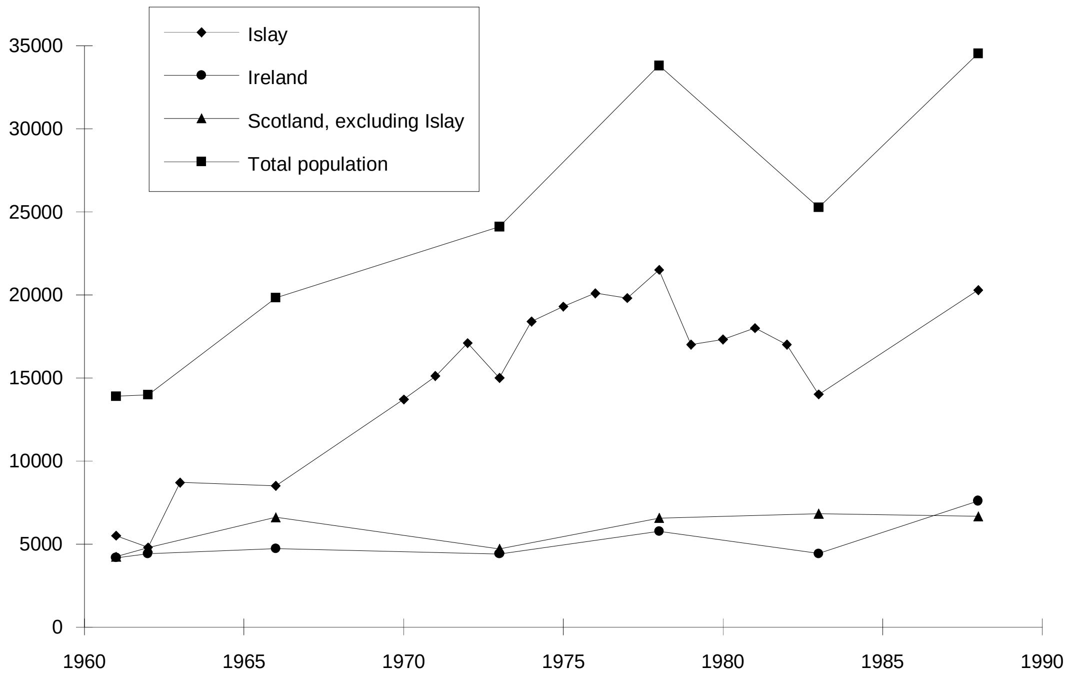


Figure 6.3. The size of the east Greenland breeding barnacle goose population censused on the wintering grounds in Scotland and Ireland. Areas other than Islay censused by aerial counts, Islay and Inishkea Islands wintering geese counted from the ground. Data from Boyd (1968), Ogilvie & Boyd (1975), Ogilvie (1983b), Fox *et al.* (1990).

The number of east Greenland barnacle geese wintering on the Inishkea Islands has also been counted regularly from the ground, and estimates of the proportion of young obtained (Cabot & West 1983).

Fig. 6.3 charts the change in size of the east Greenland breeding population over the period that air censuses of the wintering grounds have taken place. It is evident that the great increases in the total population size that took place in the three decades from 1960 are due more or less entirely to increases in the Islay wintering portion of the population. While the Islay wintering group dominates the totals there have been some variations in the number of geese elsewhere in the wintering range. The number of geese wintering on the Inishkea islands (the major Irish haunt) remained reasonably stable in the two decades to 1983, with a mean population around 2300 individuals (Cabot & West 1983). However, Fox *et al.* (1990) point out that the total number of barnacle geese wintering in Ireland has recently increased. Numbers in the Inner Hebrides, including islands near Islay, have remained fairly stable, while there has been a recent decline in the number of barnacle geese wintering in the Outer Hebrides (Fox *et al.* 1990).

Cabot & West (1983) suggest that Islay is a rather more food rich environment for the wintering geese, with greater primary production than the Inishkea Islands. For the winters 1961/2 to 1982/3 the mean percentage of first year birds on the Inishkea Islands was 6% (data of Cabot & West 1983). By contrast the mean on Islay for that period was over 13% (data from Ogilvie 1983b). While losses also appear to have been greater for the Islay population (around 10% compared to 7% for the Inishkeas, Cabot & West 1983; Ogilvie 1983b), it is this differential breeding success, combined with faithfulness to sites within the wintering range (Percival 1988) that appears to be responsible for the increase in the number of geese wintering on Islay relative to the rest of the wintering range.

Within winter movements

The movements of the east Greenland barnacle geese between different sites on the west coasts of Scotland and Ireland during the course of a winter, and their faithfulness to sites from year to year, are not known in any great detail. It appears reasonably clear that most birds are largely faithful to wintering sites from year to year (Cabot & West 1983; Percival 1988, 1991; Newton & Percival 1989). Percival's (1988) study of individually marked birds on Islay over three winters suggests that the majority of birds spend the whole winter on the island but a proportion (up to 20%) are mobile to some extent.

Ogilvie (1983b) noted that the February or March counts on Islay tend to be similar in size to, or even slightly larger than, counts the previous November. Given that reasonably large numbers of geese were being shot on Islay during the period of the counts to 1983, Ogilvie thus suggested that a move of geese onto Islay during the winter must take place. Cabot & West (1983), however, asked where these birds could come from as they saw little evidence for substantial numbers of birds moving from Irish wintering sites to Islay in the spring. In fact, little evidence in support of Ogilvie's hypothesis has been forthcoming in recent years. Newton & Percival (1989) found little evidence for a spring movement of birds from Tiree to Islay and Percival (1988) detected an influx of ringed birds in only one winter (1985/6) during the three winter period of his study.

In the winters of 1983/4 and 1984/5 intensive counts of geese arriving on Islay were carried out by Easterbee *et al.* (1987) who noted that the number of geese on the island tended to peak for about two days towards the end of October. In 1984/5 they found a second, slightly smaller, peak in November. Percival's (1988) counts throughout the winters of 1984/5, 85/6 and 86/7 also suggest that there is a peak in the number of birds on Islay towards the end of October, followed by a second influx of birds in mid-November, before numbers settle down somewhat for the winter. Percival (1988) concludes that Islay is particularly important as a staging site in the autumn before geese move to other wintering sites.

The increased proportion of the Greenland barnacle goose population that now bears individually marked rings, combined with visits to other parts of the wintering range has given some insight into the complex within winter movements. From observations of geese on Coll and Tiree, Newton & Percival (1989) found several patterns of behaviour: some birds stay the whole winter on Tiree each year, others stop on Islay in the autumn but move to Tiree or Coll by mid-winter or spring, while others change their wintering site from year to year. Newton & Percival also found that a few Islay birds visited Tiree in midwinter.

The pattern that is emerging from studies in the last decade is that the majority of east Greenland barnacle geese are faithful to a single wintering area from year to year and do not move between wintering sites in the course of the winter (though some may stage on Islay for a short time before continuing to their "real" winter destination). However, a small portion of the population may change wintering sites from one year to the next while other birds move between sites in the wintering range during the course of a single winter. These patterns have led Fox *et al.* (1990) to suggest that the optimum period to assess the distribution of Greenland barnacle geese over their wintering sites is between December and January, as this pattern should represent the distribution for the majority of the winter.

The Islay wintering barnacle geese

Islay has been the major stronghold of the wintering Greenland barnacle geese since at least 1870 (Owen, Atkinson-Willes & Salmon 1986) and, as noted above (Fig. 6.3), it is the growth of the Islay wintering barnacle goose population that has been largely responsible for the growth of the whole east Greenland breeding population. The birds arrive mainly towards the end of October each year, departing from mid-April through to May (Ogilvie 1983a). The principal roost sites are at the heads of Loch Gruinart and Loch Indaal (Fig. 6.4).

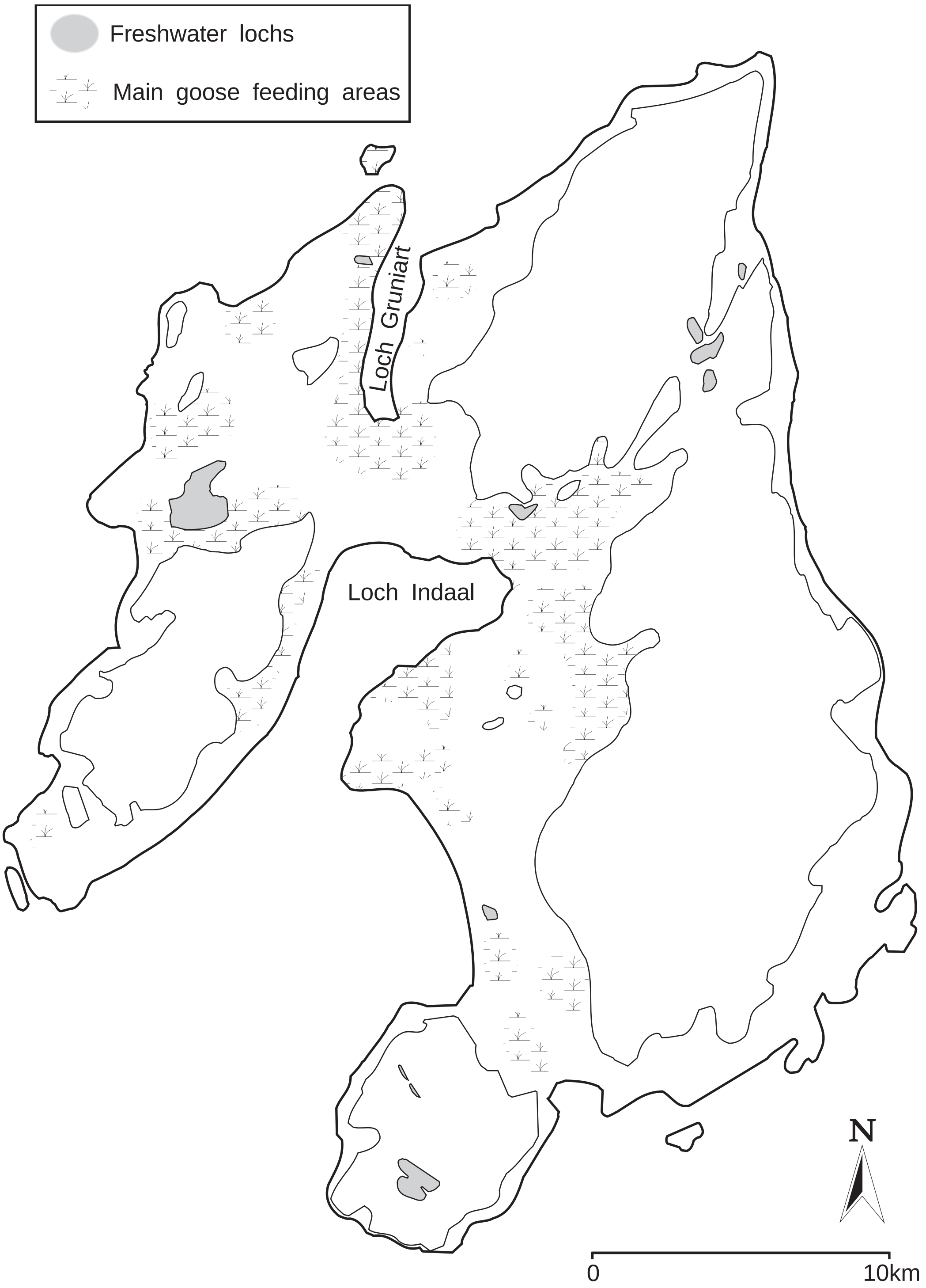


Figure 6.4. The location of the main barnacle goose feeding and roosting sites on Islay. Also shown is the 60m contour. Redrawn from Ogilvie (1983a).

The wintering barnacle geese feed almost exclusively on improved ryegrass pasture, the area of which has increased greatly since the 1950's (Owen, Atkinson-Willes &

Salmon 1986). The improvements of pastures on Islay through fertilisation and reseeding leading to extended and improved feeding opportunities for the wintering geese has undoubtedly been a major reason for the large increases in the Islay wintering barnacle goose population in three decades since 1960 (Ogilvie 1983a; Owen, Atkinson-Willes & Salmon 1986). While the link has yet to be established conclusively, it is likely that the higher quality winter feeding on the resown Islay pastures is largely responsible for the difference in breeding success between Islay and Ireland wintering birds discussed previously (where the success of birds wintering on the Inishkeas in Co. Mayo may only be 50% of that of Islay wintering birds) (Cabot & West 1983; Ogilvie 1983b). Similarly, Newton & Percival (1989) noted that the proportion of young in barnacle goose flocks wintering on Tiree was often less than that observed in Islay wintering flocks. Another factor, of course, that may influence these differences in breeding success is continued segregation on the breeding grounds of birds that winter in different areas. Cabot *et al.* (1984) report that significant differences in breeding success exist between different nesting areas in Greenland.

From observations of individually ringed geese, Percival (1988, 1991) found that birds are not only faithful to Islay as a wintering site but are faithful to restricted feeding areas within Islay both during a winter, and from year to year. Percival also found some evidence that the breeding success of the different groups wintering on Islay is different and suggests that this is not readily explained by differences in winter feeding on the sites but may be due to continued association throughout the year of birds from each site.

However the distribution of wintering geese across Islay is not constant throughout the course of the winter. Easterbee *et al.* (1987) suggest that the birds tend to concentrate in the Loch Gruinart area on arrival on Islay before dispersing to other parts of the island, and presumably, given the peak in the number of birds on Islay in late October, to other parts of the wintering range. The distribution of barnacle geese over Islay during the winter of 1989/90 is shown in Fig. 6.5. Each of the three counts is the mean of two counts made on consecutive days (Easterbee *et al.* 1991). In addition to the changes through the course of the winter apparent from Fig. 6.5, changes in distribution were also recorded between the two days of each of the three counts. Weather conditions were not always the same for the counts and Easterbee *et al.* attribute some of the variation between the counts on consecutive days to this fact.

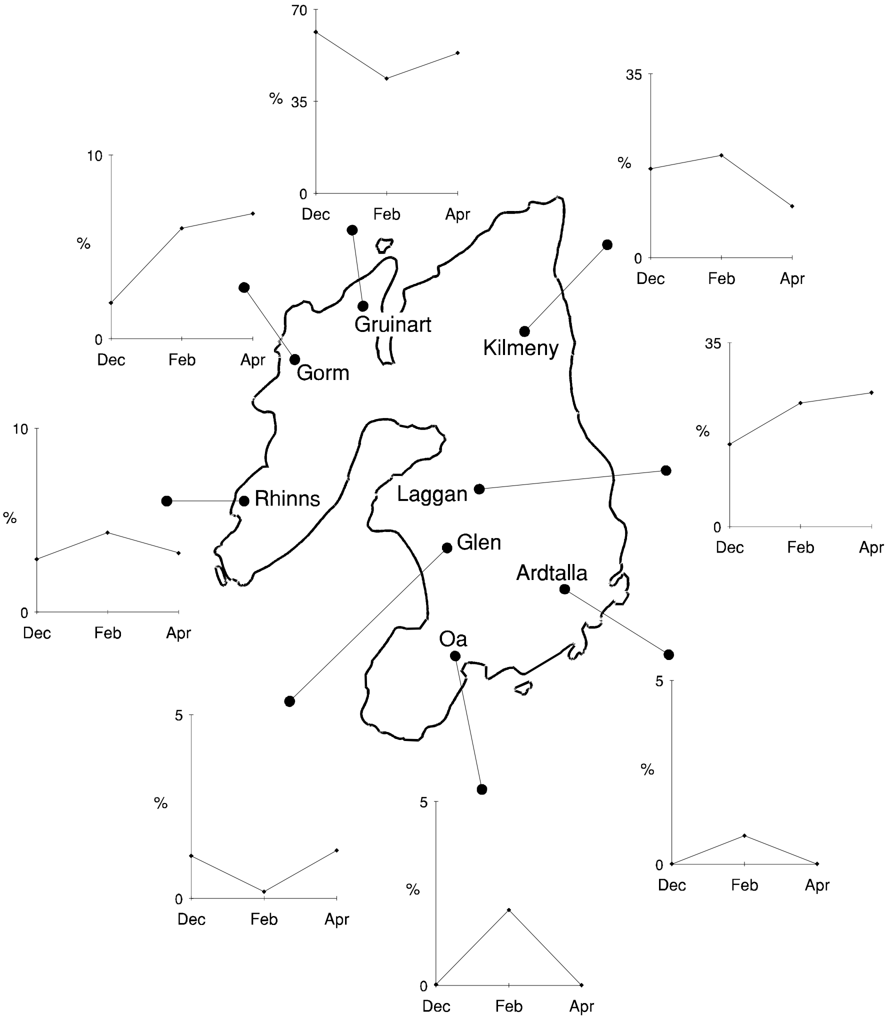


Figure 6.5. The distribution of barnacle geese over different areas of Islay for the winter 1989/90. Each point is the mean of two counts on consecutive days (3/4 December 1989, 10/11 February 1990, 1/2 April 1990) expressed as the percentage of barnacle geese recorded on the island at that time. Data from Easterbee *et al.* 1991. Mean numbers on the island for the two counts in December, February and April were 24861.5, 23093.5 and 21993 respectively.

Agricultural damage

Given that the large numbers of barnacle geese wintering on Islay are feeding almost entirely on agricultural land, some conflict with agricultural interests is inevitable. Ogilvie (1992) reports that barnacle geese were recorded as doing "great damage to grass" as early as the 1890's.

Percival (1988, 92) studied the effects of goose grazing on agricultural grasslands on Islay. Comparing grazed and neighbouring ungrazed (fenced) plots, Percival found that at all sites studied in three winters there was a significant reduction in grassland yield after grazing by geese. He found that newly reseeded grasslands tended to attract the greatest number of geese and thus suffered the greatest reduction in yield. Winter goose grazing also reduced the yield of silage cut in June. However, due to the great variation in yield of different areas, Percival was not able to associate a given amount of goose grazing (as measured by dropping counts) with a given yield loss. Year to year variation in grassland production meant that the areas with greater goose grazing may have lower yields than areas with less grazing in some years, but higher yields in other years. Percival suggests that the presence of grazing barnacle geese may make up to 80% of early spring grass growth unavailable to farm stock. He also found that, in addition to the direct loss in spring grass and silage yields due to goose grazing, yield was further reduced by the delays in the application of fertiliser caused by the presence of geese. The magnitude of the yield loss found by Percival was slightly less than that of a previous study on Islay by Patton & Frame (1981). Patton & Frame suggest that goose grazing may also result in the need to reseed fields at more frequent intervals.

Percival (1988) demonstrated that the Islay wintering barnacle geese show a strong preference for feeding on newly reseeded fields, and that fertiliser application may also increase goose grazing (though this depended on the original nutrient status of the field). A similar preference for improved pasture was noted by Bignal, Curtis & Matthews (1988). Despite their willingness to move to reseeded fields, Percival (1988, 1991) found that many individuals tended to be faithful to a relatively restricted range of feeding sites on Islay.

Reviewing several studies (including those of Percival (1988)) of agricultural damage resulting from grazing by several goose species in different areas, Patterson (1991) concludes that there is ample evidence of significant losses in both grass and cereal crops at a wide range of goose grazing levels, but suggests that the wide variability in losses makes it unlikely that losses could be adequately predicted from observed levels of goose grazing.

Brodie (1991) points out that the agricultural economy of Islay is based entirely on grass production supporting cattle and sheep. Geese therefore compete directly with cattle for early spring grass growth. Brodie (1991) suggests that financial losses, in addition to the necessity of purchasing extra winter feed, are incurred by farmers as a result of delays in fertiliser application which lead to poorer quality fodder, and, therefore, poorer milk yields and poorer condition of livestock at sale.

Thus there appears to be ample evidence that, for at least some farmers on Islay, the agricultural and financial implications of the wintering barnacle geese may be quite serious. Brodie (1991) points out that island farmers are already disadvantaged, relative to their mainland counterparts, by the costs of transporting feed and fertiliser to the island and livestock to the mainland markets. On a national scale agricultural damage by wildfowl is negligible. However the damage tends to be localised and individual farmers may suffer badly. Even within Islay there are considerable differences in the degree to which farmers are affected by grazing of wintering barnacle geese.

Shooting

Shooting of wintering barnacle geese was permitted on Islay during December and January from 1955 (Owen, Atkinson-Willes & Salmon 1986). In 1976 the open season was extended from these two months to five (Owen, Atkinson-Willes & Salmon 1986). While increasing agricultural damage by the growing barnacle goose population was cited as the main reason for this change, Bignal, Stroud & Easterbee (1991) report that shooting towards the end of the 1970's was largely commercial sport shooting organised by the major Islay estates and hotels. The annual kill of barnacle geese in the late 1970's and early 1980's has been estimated at 1500–2000 individuals, up from previous levels of 500–700 birds a year (Elliot 1989).

This situation changed in 1981 with the introduction of the Wildlife and Countryside Act which banned sport shooting of barnacle geese. However, under this act a licence to shoot geese in order to scare flocks from agricultural land may be issued if there is serious damage to livestock, foodstuff for livestock, crops or vegetables (Brodie 1991). Licences are issued to farmers after assessment by members of the agricultural inspectorate and consultation with local Nature Conservancy Council staff (Brodie 1991).

Management of the conflict between agriculture and conservation

The relationship between agricultural interests concerned at the financial implications of the growing number of wintering barnacle geese on Islay, and conservation interests pleased to see the population flourishing, has often been rather acrimonious since the introduction of the 1981 act. The conflict has reached the national newspapers in several winters in recent years. The problem, essentially, is how to implement the conservation management of the wintering barnacle goose in line with the requirements of national and European law (and recognising the birds as part of the natural heritage) without putting the farmers on whose fields the geese graze at a significant financial disadvantage.

Since 1981 the management policy on Islay has been one of refuge provision. This takes the form of Sites of Special Scientific Interest (SSSIs) declared because of their importance to the wintering geese. These have been supplemented by the Royal Society for the Protection of Birds' (RSPB) purchase of the farmland around Loch Gruinart which is the most important area on the island for the wintering barnacle geese (Easterbee *et al.* 1987). Farmers within SSSIs receive compensation for the effects of goose grazing on their land. The main problem with this management policy has been the fact that in some years almost half of the wintering geese feed outside SSSI and other refuge areas in early spring (Brodie 1991). Brodie (1991) suggests that the proportion of geese remaining in refuge areas throughout the winter is higher in winters with better grass production. The unfortunate consequence of this is that it is in the harder winters, in which grass production for livestock is most limited, that the geese tend to graze more outwith refuge areas, thus producing heightened conflict.

The management policy on the RSPB reserve has been to farm the land in such a way as to produce pastures of a quality designed to attract the maximum possible number of feeding geese. Owen (1977) suggested that the Greenland barnacle goose population would become limited by factors acting on the breeding grounds and that a relatively small reserve area could thus provide sufficient feeding to accommodate the population when damage to farmland was most likely. However, as a result of the faithfulness to feeding sites shown by the wintering barnacle geese (Percival 1988, 91) the movement of geese to the RSPB reserve has been less than was hoped. Attempts have been made to scare the geese from fields outwith the refuge areas (Percival, Halpin & Houston 1988; Ogilvie 1992) by organised groups as an more systematic scaring measure than the issuing of licences to shoot geese. While this appeared successful initially (Percival, Halpin & Houston 1988) with a movement of birds onto refuge areas, some reversal of this trend may have occurred (Bignal, Stoud & Easterbee 1991). The success of the organised scaring scheme is still a matter of some doubt (Ogilvie 1992).

A basic premise of the provision of refuges for the wintering geese must be that, at some stage, density dependent regulation of the population will occur. To date no such regulation of the east Greenland breeding barnacle goose population has been detected (see section on *population dynamics* below) and the general trend of the Islay wintering population is still one of increasing numbers (Fig. 6.6a). If it is true that the primary reason for the increase in numbers of the Islay wintering barnacle geese is the availability of improved pastures leading to heightened breeding success relative to the rest of the wintering range (Ogilvie 1983a; Owen, Atkinson-Willes & Salmon 1986), then a "worst case" view of the refuge policy is that it merely serves to increase Islay's 'carrying capacity' for wintering barnacle geese. Given the observed faithfulness of the geese to feeding sites on the island (Percival 1988, 91) then the increased area of improved pasture provided by the refuge areas may serve only to exacerbate the problem, leading to increased numbers of geese which disperse from refuge areas in search of better feeding when food becomes scarce. It is conceivable that the numbers of wintering geese may ultimately be limited by the availability of winter feeding rather than factors on the breeding grounds. Faced with the apparently continuing upward trend in goose numbers, many Islay residents have called for the numbers of wintering barnacle geese to be reduced and regulated (Brodie 1991). In other parts of Britain too, farmers previously keen to work with conservation bodies in goose management have joined in calls for population control in the face of continuing increases in the size of many goose populations (see discussion in Owen & Pienkowski 1991).

As mentioned above, a major cause of friction between conservation and agricultural interests on Islay has resulted from the fact that goose grazing is not restricted to the refuge areas but compensation payments (other than payments to help provide scaring) are restricted to these areas. Bignal, Stroud & Easterbee (1991) point out that the original Brigend Flats SSSI proposed in 1971 would have included feeding areas in the Ballygrant valley (which are the focus of much of the barnacle goose grazing that occurs outwith refuge areas), but was restricted to the roost areas after consultation with the owners, Islay Estates. In retrospect it would appear that this omission, which presumably resulted from moves to protect sport shooting access, is responsible for much of the "two-tier system" that excludes some farmers from compensation payments. The issue of sport shooting of wintering barnacle geese on Islay, while officially outlawed, has continued to cause friction among conservationists and "agricultural" interests. Indeed, it appears that some licences issued for the purpose of scaring geese have actually been used to enable sport shooting, with the result that the prevention of agricultural damage through scaring has not really occurred (Bignal, Stroud & Easterbee 1991; Haigh 1984).

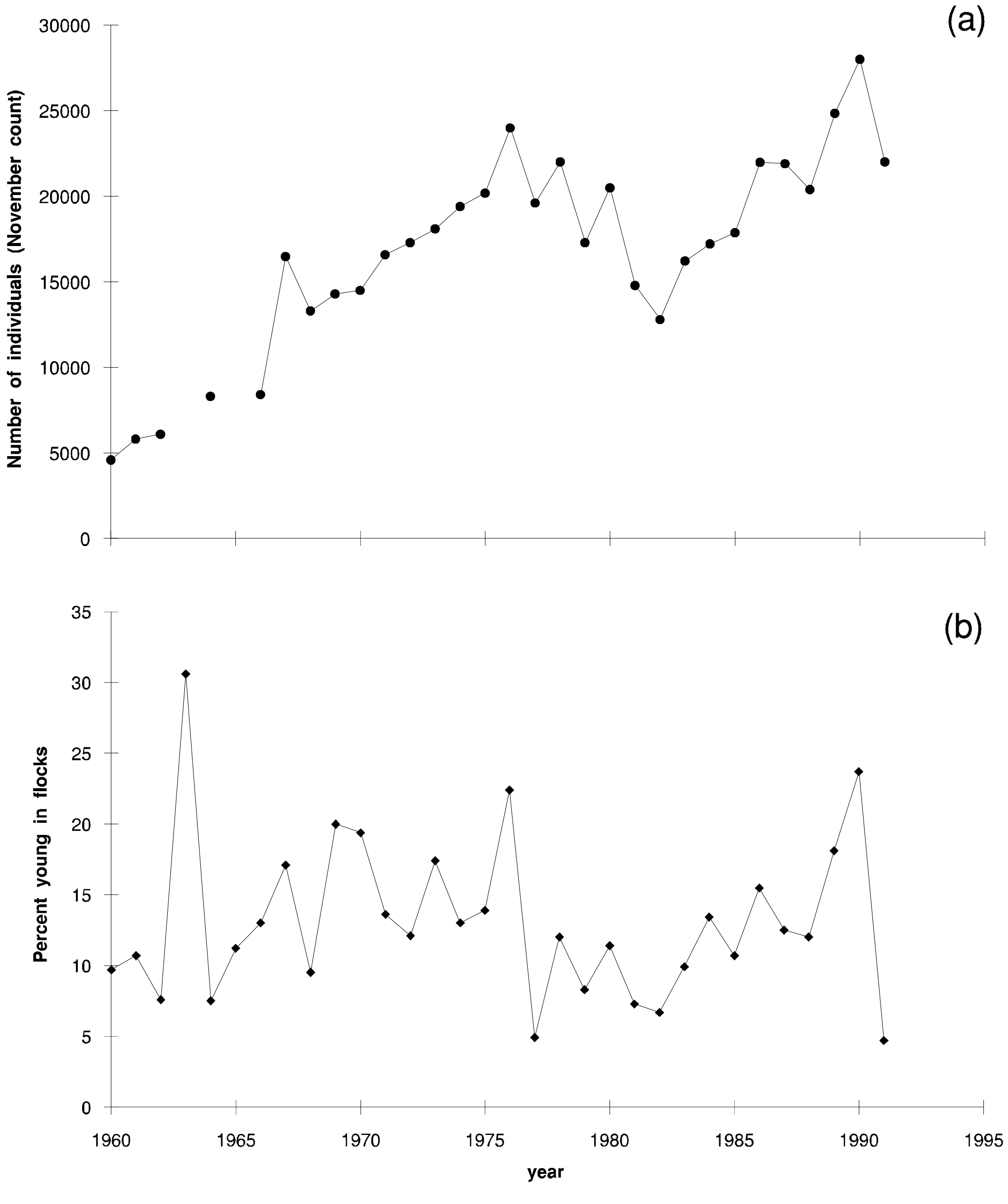


Figure 6.6. The basic population data for the population of barnacle geese wintering on Islay: (a) the number of wintering geese counted in November, and (b) the proportion of first year birds in the flocks arriving on Islay. Data from Boyd (1968), Ogilvie (1983,92), and Nature Conservancy Council counts.

The issue of realistic compensation for farmers outwith SSSIs suffering goose damage has been hindered by the fact that it has proved impossible to associate a given level of goose grazing with a certain level of damage (Percival 1988; Patterson 1991). Farmers and conservationists have disagreed over the problem of perceived versus actual reduction in the grazing available to livestock as a result of goose feeding (Owen 1990a). A possible way forward may have been provided by the recent Scottish Natural Heritage Act, which empowers Scottish Natural Heritage (the successor to the Nature Conservancy Council for Scotland) to offer management payments to farmers whose land is outwith SSSIs (A. J. Kerr, pers. comm., Ogilvie 1992).

Population dynamics

Fig. 6.6a,b shows the times series of the "raw data" relating to the population of barnacle geese wintering on Islay: the November count data, and the proportion of first winter birds in the flocks, assessed during the November count. The remainder of this section investigating the population dynamics of the Islay wintering portion of the Greenland barnacle geese will use only this November count data. This is for two reasons: the November count data is the longest series of counts available (though count methods have been adapted to cope with the larger numbers of wintering geese over the course of the period 1960–91), and the proportion of first year birds year birds in the flocks is assessed around this time. As discussed previously, there is growing evidence that Islay as used as a staging area in the autumn by more geese than subsequently spend the majority winter on the island. This has led to suggestions that the November counts may be susceptible to anomalies where counts may have coincided with large numbers of staging birds being present on the island in some years and not others (Easterbee *et al.* 1987). However the data of Easterbee *et al.* (1987) and Percival (1988) suggests that the main peak of staging birds will generally have left the island by the time of the November counts. Fig. 6.7 demonstrates that, for years for which such data are available, the November counts are closely related to both the mean and maximum numbers of barnacle geese overwintering on Islay.

The proportion of first winter birds in barnacle goose flocks wintering on Islay is highly variable (Fig. 6.6b). Ogilvie (1983a) attributed this wide observed range in breeding success to weather in spring and summer in Scotland, Iceland and

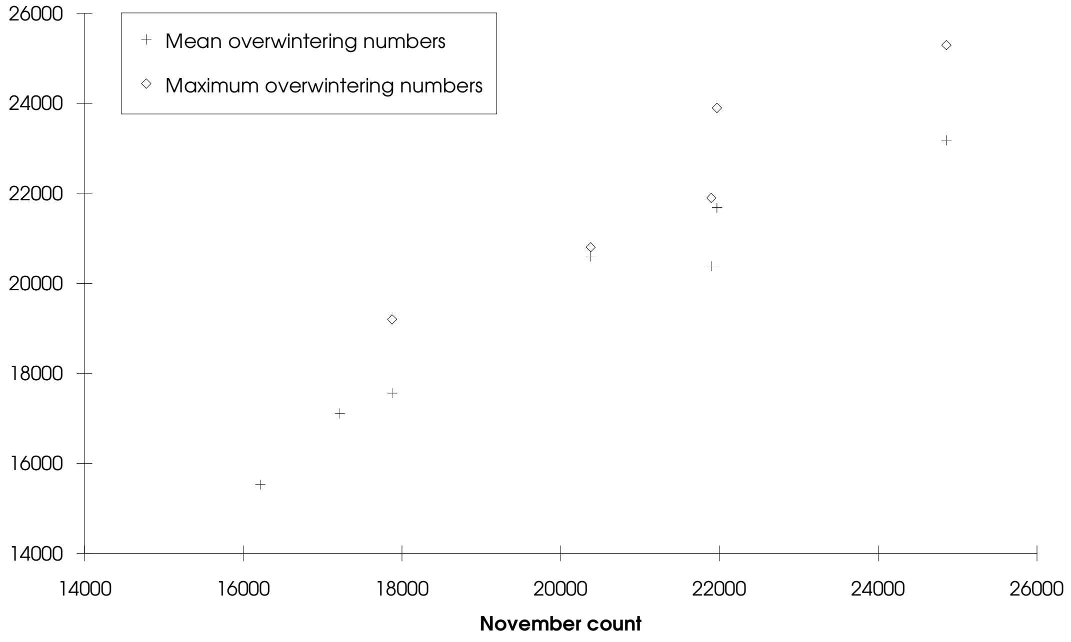


Figure 6.7. The relationship between mean and maximum numbers of barnacle geese wintering on Islay, and November count. Mean overwintering numbers for 1983/4 to 1989/90 from Bignal, Stroud & Easterbee (1991, Table 4.1); maximum numbers for 1985/6 to 1989/90 from Kirby, Waters & Prys-Jones (1990).

Greenland. This was investigated by Fox & Gitay (1991) who gathered meteorological data from the Hebrides, Iceland and east Greenland and carried out a multiple regression investigation of the effect of these meteorological variables on the breeding success of the Islay wintering barnacle geese. Fox & Gitay suggest that up to 60% of the variance in breeding success can be attributed to weather conditions in Scotland in spring, in Iceland during staging, and on arrival in Greenland. However, while Fox & Gitay use a measure of breeding success based on the proportion of young in flocks overwintering on Islay, they only incorporate meteorological data for January to July in their analysis. It is likely that the effects of weather on the autumn migration from the breeding to the wintering grounds will also contribute to the numbers of first winter birds recorded on the breeding grounds. If meteorological variables for this part of the year had also been included in the analysis it is conceivable that even more of the variance in breeding success could be attributable to the effects of weather.

The dominant feature of the November count time series (Fig. 6.6a), after the dominant upward trend in numbers discussed previously, is the general decline in the

Islay wintering population in the period 1977 to 1983. This decline is generally attributed directly to the increased overwintering mortality caused by the increased shooting activity in the late 1970's (Owen, Atkinson-Willes & Salmon 1986; Owen 1990b; Fox *et al.* 1990; Bignal, Stroud & Easterbee 1991).

Some insight into the causes of the fluctuations in the size of the population of barnacle geese wintering on Islay in the period 1961–1991 can be gained by considering the year to year changes in *per capita* recruitment and mortality. The wintering barnacle geese in the November of any year, t, can be partitioned into juveniles (first winter birds), j_t, and adults (non first winter birds), a_t, simply given by

$$\begin{aligned} j_t &= y_t N_t \\ a_t &= N_t(1 - y_t) \end{aligned} \tag{6.1}$$

where N_t is the number of birds counted in the November of year t, and y_t is the proportion of first year birds in the wintering flocks. To estimate recruitment and mortality from these data some assumptions must be made, the first of which is that the Islay wintering barnacle geese represent a closed population. While the Islay birds are, of course, just a part of the east Greenland breeding barnacle goose population there is, as discussed above, increasing evidence that individuals are faithful to wintering sites from year to year, and that such segregation may be present on the breeding grounds as well. Given this assumption, the mortality rate from the November count in year t to the November count in year t+1 is given by

$$m_t = 1 - \frac{a_t}{N_{t-1}} \tag{6.2}$$

where a_t/N_{t-1} is the *per capita* survival from the November of year t–1 to the November of year t. Mortality estimates are not independent from year to year as the population size in a given year appears in the numerator of the fractional part of eqn. [6.2] in one year and the denominator the next. Ebbinge, van Biezen & van der Voet (1991) suggest that while individual survival estimates may be inaccurate, the mean will be reasonably accurate as the appearance of a population count in the numerator one year and denominator the next will lead to a cancelling out of counting errors. For the Russian breeding barnacle goose population Ebbinge, van Biezen & van der Voet found that the mean survival rates estimated by the method considered here were very close to estimates derived from the resighting of ringed individuals.

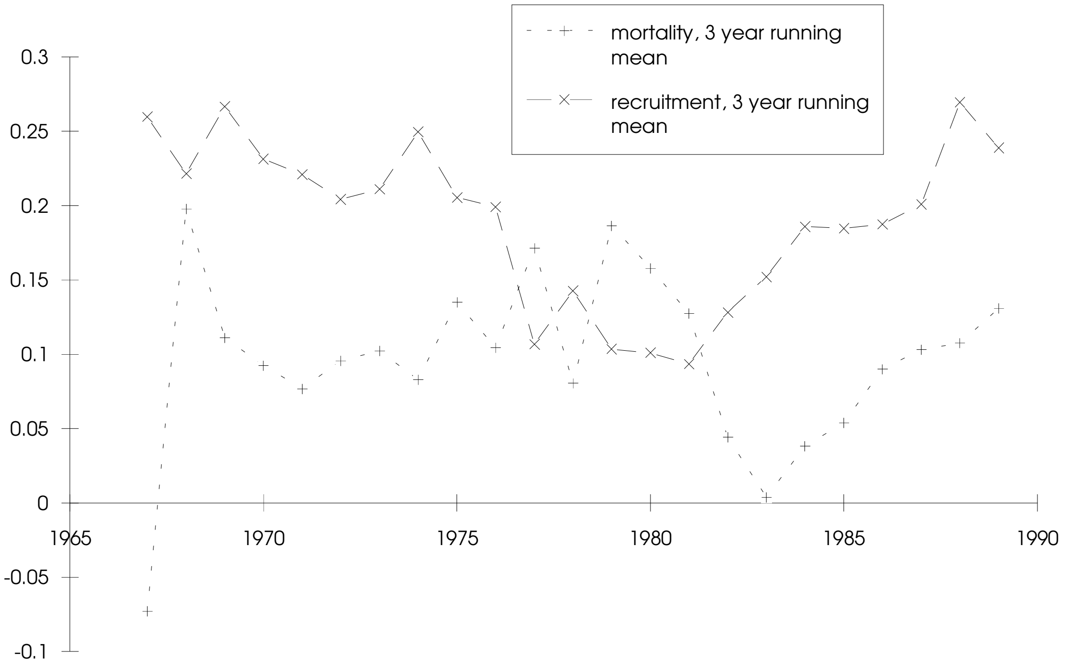


Figure 6.8. Three year running means of recruitment (calculated from [6.3]) and mortality (calculated from [6.2]) the November count data for the Islay wintering barnacle geese. Data from Boyd (1968), Ogilvie (1983,92), and Nature Conservancy Council counts.

Assuming that the age of first breeding is three years then the number of adult birds, a_t, in a winter *t* represents three groups: second winter birds that will not breed the following spring, $a_{2,t}$, third winter birds that will breed for the first time the following spring, $a_{3,t}$, and older birds, $a_{4+,t}$. The number of birds in the November of year *t* that have the potential to breed the following year is thus given by $a_{B,t} = a_t - a_{2,t}$. Making the further assumption that the survival rate is the same for birds of all ages the number of second winter birds can be is given by $a_{2,t} = j_{t-1}s_{t-1}$ where s_{t-1} is the *per capita* survival rate, a_t / N_{t-1}, considered above. The recruitment rate is then given by

$$b_t = \frac{j_{t+1}}{a_{B,t}} \qquad [6.3]$$

Fig. 6.8 compares three year running means of recruitment and mortality rates for the period of the available November count data. This demonstrates that mortality does indeed exceed recruitment in four of the six years during the period 1976 to 1981 when the more liberal shooting regime was in place on Islay. However, while mortality during this period was above average, an equally important reason for the observed decline in numbers of Islay wintering geese was the low recruitment rates in the late 1970's and early 1980's. Ogilvie (1983b) recognises that poor breeding successes as well as increased shooting contributed to the decline in numbers from 1980–1983. Fox *et al.* (1990) assert that the poor breeding success observed in the late 1970's and early 80's is probably attributable to geese reaching the breeding grounds in poorer condition as a result of the increased disturbance, due to shooting, in this period. Fig. 6.8, however, suggests that breeding success was in decline from the mid-1970's, before the increased shooting was permitted, and that it did not reattain its pre-1975 level until the mid-1980's, some time after shooting was restricted by the Wildlife and Countryside Act of 1981. This tends to suggest that the poor breeding results during these period are not solely attributable to increased shooting on the wintering grounds. It would be interesting to examine the residual variances from the multiple regression of breeding success on meteorological variables carried out by Fox & Gitay (1991) to see if less of the variation in the proportion of young on the wintering grounds is attributable to the weather during the period of increased shooting from 1976 to 1981. Unfortunately Fox & Gitay do not give sufficient detail in their paper to do this without additional information.

For the period since the Wildlife and Countryside Act came into force, the number of geese shot under licences issued to farmers suffering agricultural damage has had to be reported (Feare 1991). While some doubts have been raised regarding the reliability with which the numbers shot are reported (Appleby 1991) others (Feare 1991) feel that reporting is reasonably accurate. Other than the general view that prior to 1976 500-600 birds were shot annually increasing to 1500 to 2000 in the late 1970's (Elliot 1989) the numbers shot under licence provide the only published data on shooting levels. Using these data the effect of the numbers shot on recruitment and mortality is investigated in Fig. 6.9. It is apparent from Fig. 6.9a that there is little relationship between mortality and the number reported shot. This suggests that the overwintering mortality due to shooting (which Owen (1990b) suggested is the main source of overwinter mortality) is less important in determining overall mortality than deaths at other times of the year. Owen & Black (1991) suggest that mortality on the autumn migration is the major source of mortality affecting the Svalbard breeding barnacle goose population. It is likely that migration mortality also contributes substantially to the annual mortality of the Islay wintering barnacle geese. Mortality, as calculated from [6.2], is actually negative in two years. There is, of course, no way of knowing whether these "impossible" values are due to counting errors or the interchange of individuals between different areas of the wintering range from year to year.

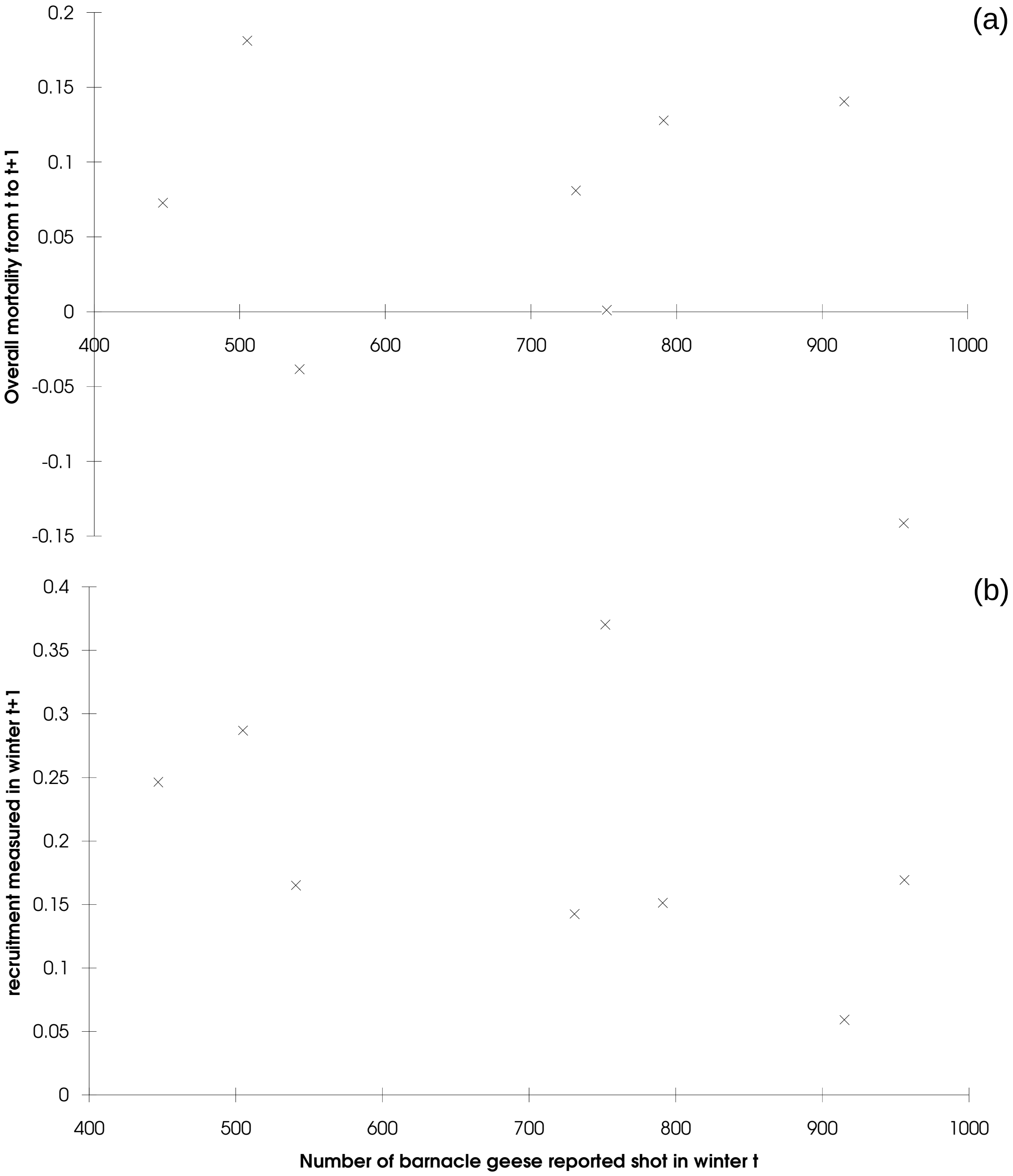


Figure 6.9. The relationship between reported numbers of barnacle geese shot under licence on Islay in a given winter, *t*, (1982/3 to 1989/90) and (a) mortality (from the November count in winter *t* to the count in winter *t*+1) and (b) recruitment (based on counts in winter *t*+1), calculated from eqns. [6.2] and [6.3] respectively (shooting data from Brodie 1991).

Fig. 6.9b also shows little evidence of a strong relationship between breeding success and the number of geese reported shot the previous winter. This is not really surprising in the light of Fox & Gitay's (1991) suggestion that at up to 60% of the

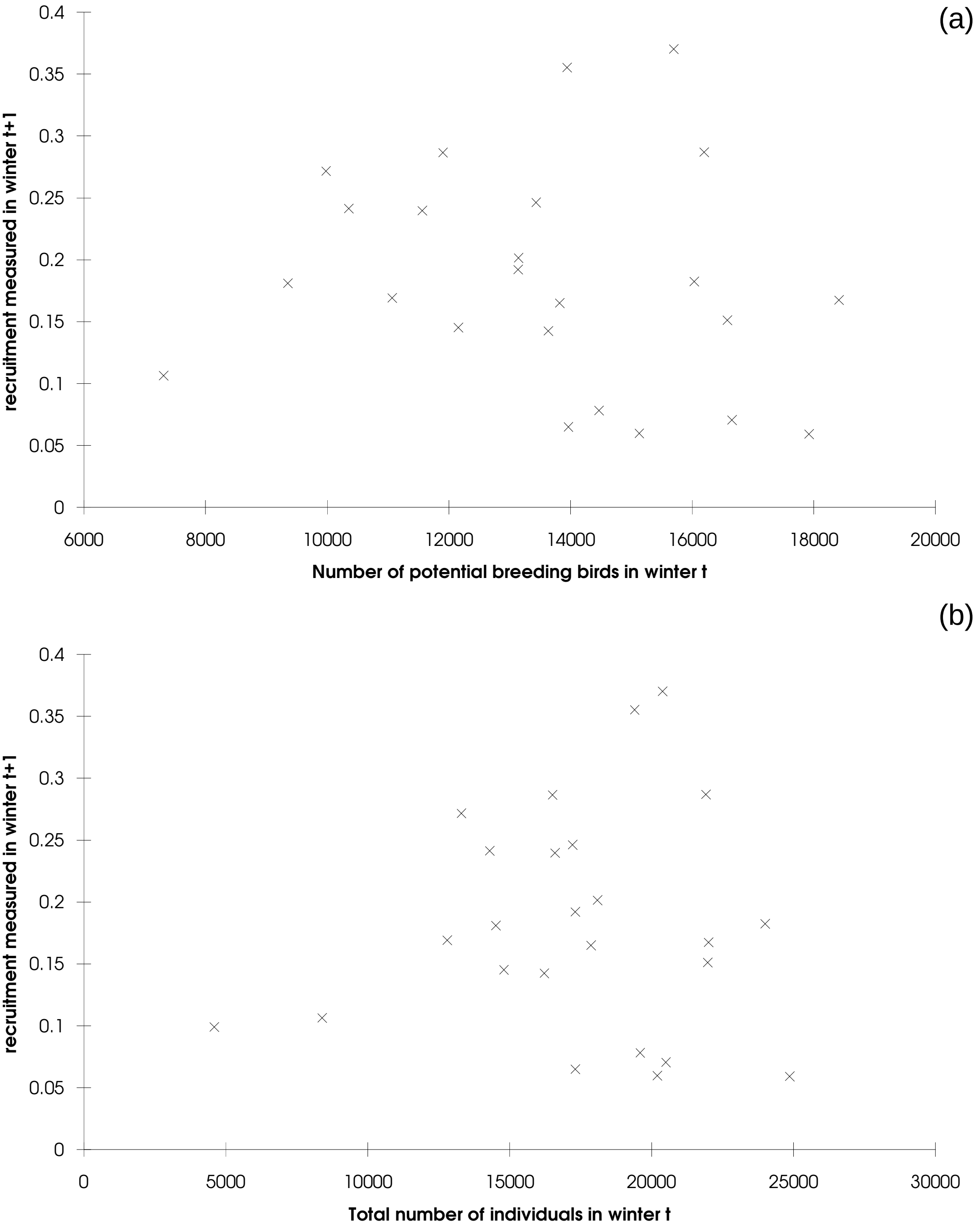


Figure 6.10. The relationship between recruitment (based on the proportion of first year birds in a year t+1), given by [6.3] and (a) the number of potential breeders in winter t, $a_{B,t}$, and (b) the total number of individuals in winter t.

variance in breeding success may be attributable to the weather conditions encountered by the geese in the first half of the year.

Overall then, it would appear that, despite common assertions to the contrary (Owen, Atkinson-Willes & Salmon 1986; Owen 1990b; Fox *et al.* 1990; Bignal, Stroud & Easterbee 1991), the evidence that shooting plays a major role in determining the dynamics of the Islay wintering barnacle geese is actually rather weak.

Another aspect of the population dynamics that must be considered is whether recruitment and mortality are affected by population size. While the limitation of population size either by lack of feeding on the wintering grounds or competition for nesting sites or food on the breeding grounds will inevitably limit the Greenland breeding barnacle goose population, there is little published evidence that such factors have been operating in recent years. Fox & Gitay (1991) found no evidence of density dependence operating in breeding success: the number of successfully breeding pairs was directly related to the size of the breeding population over a range of population sizes. In fact, there is little evidence for density dependent regulation of population growth in any of the British wintering goose populations (Owen 1990a; Summers & Underhill 1991), with the exception of the Svalbard breeding barnacle goose population which has recently shown a density dependent decline in recruitment (Owen & Black 1989). Figs. 6.10 to 6.12 investigate possible density dependence in the November count data.

Fig. 6.10a demonstrates that there is no relationship between the recruitment determined by the proportion of individuals in a given winter, *t*+1, (measured by [6.3]) and the number of potential breeders in the previous November, $a_{B,t}$. Similarly, recruitment shows no relationship to the total number of individuals (potentially breeding adults, and first and second winter birds).

Fig. 6.11 considers the relationship between survival from the November count in one winter (*t*) to the count in the next winter (*t*+1), and the population size in the first winter (*t*). The initial impression from this figure is one of a decrease in year to year survival as population size increases. However, it should be noted that the highest values of survival are all "impossible" values, greater than one. These values occur when population size is small, which places them near the beginning of the time series (the highest survival value, 1.63, occurred from 1966/7 to 1967/8). It seems likely, therefore, that part of the reason for these very high values can be attributed to less accurate census techniques in the early years of the time series. Restricting attention to those survival values less than one (for which population sizes are in the

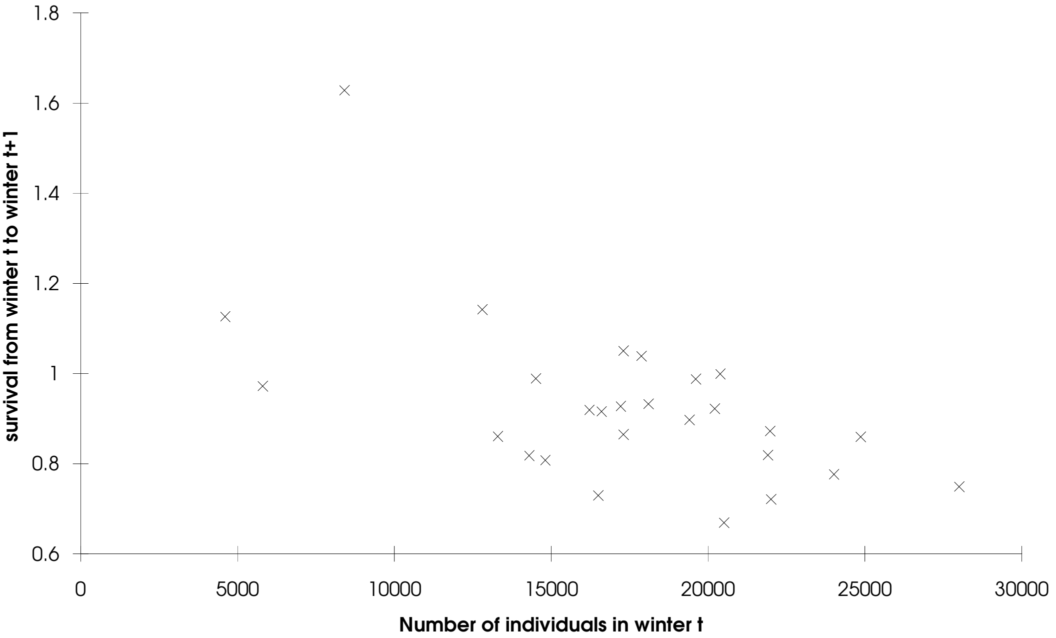


Figure 6.11. The relationship of survival from one winter to the next and population size, in barnacle geese wintering on Islay.

region 12500 to 28000 individuals) reveals little evidence of a relationship between survival and population size.

Finally, consider the relationship between population size and the logarithmic population growth rate:

$$r_t = \ln\left(N_{t+1} / N_t\right) \tag{6.4}$$

This is shown in Fig. 6.12. The growth rate appears to decline with population size, but this impression is again influenced greatly by outlying points, in particular the high growth rate recorded from the November count in 1966 to the count in November 1967. This corresponds to the very high survival rate in Fig. 6.11. For population sizes in the range 10000 to 30000 individuals (a range which includes all but three of the calculated values of r_t) there is little evidence of a decrease in population growth rate with population size. Thus, at current population sizes, there is little evidence of density dependent effects in the dynamics of the Islay wintering barnacle geese.

In summary, it would appear that the population dynamics of the Islay wintering barnacle geese are strongly influenced by the apparently random influence of the

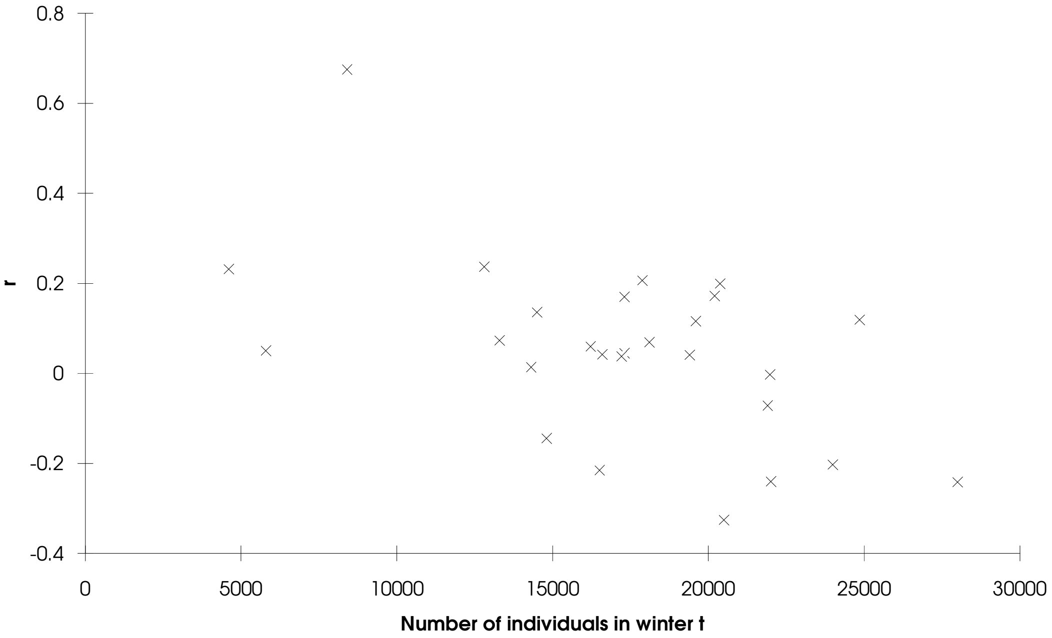


Figure 6.12. The relationship between population size in winter *t* and the logarithmic growth rate, r_t, given by eqn. [6.4], for the November count data for barnacle geese wintering on Islay.

weather. While shooting on the wintering grounds can be a significant source of mortality, the level of shooting does not appear to determine overall annual mortality, which may be determined to a large extent by mortality on the autumn migration. There is little evidence to link shooting on the wintering grounds with breeding success, which also appears to be influenced heavily by weather conditions (Fox & Gitay 1991). At current population sizes there is little evidence of density dependent regulation. While such regulation would undoubtedly begin to act more obviously should the population continue to grow, it is possible that any current density dependence operating is being masked by the stochastic influence of the weather on the population growth rate.

Before leaving this discussion of the dynamics of the Islay wintering barnacle geese, I would like to investigate one other possible feature. Note however that, given the data currently available, this amounts to little more than speculation: hence its position at the end of this chapter. Considering again the time series of Fig. 6.8, a certain amount of symmetry in the 3 year running means of recruitment may be discernible. It is tempting, if perhaps rash, to suggest that the low recruitment rates in the late 1970's and early 1980's may represent a trough in a rate which is varying in a cyclic (or at least quasi-cyclic, *sensu* Nisbet & Gurney (1982)) manner, rather than

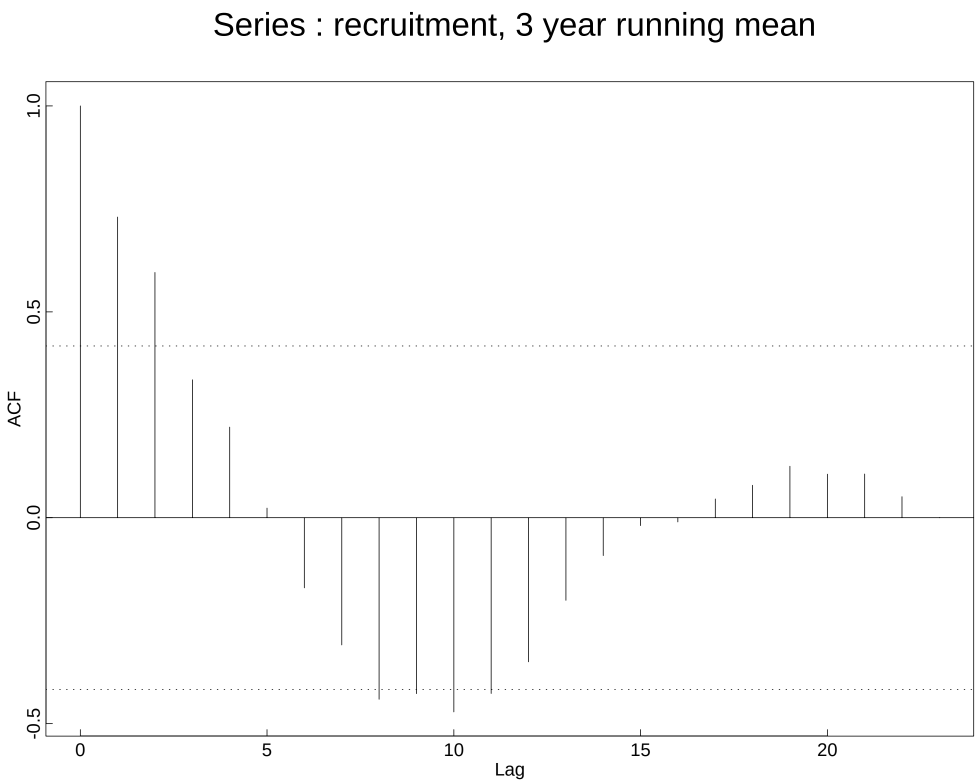
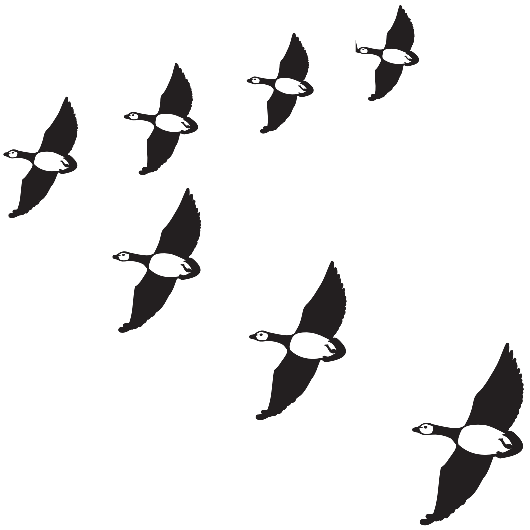


Figure 6.13. The autocorrelation function of the 3 year running mean (Fig. 6.8) of recruitment in the Islay wintering barnacle geese calculated, using [6.3], from the November count data. Lags in years. The dotted lines mark approximate 95% confidence intervals for the hypothesis that the autocorrelation is not significantly different from zero. Note that the length of the time series of recruitment rates does not really justify calculating autocorrelation at the longer lags illustrated here and that this figure must therefore be treated with some scepticism.

simply fluctuating around some mean level. This can be investigated further by calculation of the autocorrelation function (Fig. 6.13).

While the shape of the correlation function is basically in line with the idea that the recruitment rate is somewhat cyclic, it must be emphasised that calculating the autocorrelation for lags that are similar in length to that of the time series has little validity. Given that the period of the speculative cycles in recruitment is of the order of 15 to 20 years, it will require considerably more years of data collection before it could be stated with any real justification that the poor breeding success of the Islay wintering barnacle geese during the late 1970's and early 80's was indeed due to some cyclic variation rather than simply a run of poor years. However, it is interesting to note that the breeding success in 1992, determined by the proportion of young in wintering flocks on Islay, appears to be low (S.M. Percival, pers. comm.). This follows the lowest breeding success ever recorded, in 1991 (Ogilvie 1992).

If quasi-cyclic variation in recruitment in the Islay wintering barnacle geese is ever established, what are possible causes ? Summers & Underhill (1987) found good evidence for a three year cycle in breeding success in brent geese (*Branta b. bernicla*) which breed on the Taimyr Peninsula. This appears to be related to the well established three year cycle in lemming (*Lemmus sibiricus* and *Dicrostonyx torquatus*) numbers in the area, with a poor breeding year in the geese following a year in which a peak in lemming numbers occurred and good goose breeding success when lemming numbers are high. The explanation offered for this pattern is that predators, such as the arctic fox (*Alopex lagopus*), are forced to switch to feeding on goslings when lemming numbers crash (Dhondt 1987; Summers & Underhill 1987). Cabot *et al.* (1984) reported that, in the summer of 1984, arctic foxes were responsible for the deaths of as much as 43% of barnacle goose goslings surviving the jump from some nesting cliffs in Greenland. They suggest that barnacle goose breeding success may be related to the abundance of arctic foxes, which in turn may be related to the numbers of lemmings in the area. However, the cycle period in arctic foxes in Greenland averages four years (Angerbjörn *et al.* 1991, and references therein). It is not immediately apparent how this would relate to cycles of longer periods in barnacle goose recruitment. Given that the existence of such cycles is, at best, highly speculative it is, therefore, probably not necessary to worry too much about their causes at this time.



Chapter 7

An assessment of shooting as a tool in the management of the Islay barnacle geese

In this chapter the use of controlled shooting in the management of the population of barnacle geese wintering on Islay is investigated. This follows the increasing calls in recent years from farmers on Islay for a cull to regulate the continuing trend of increasing numbers of geese wintering on the island. As the analyses of the previous chapter showed, there is relatively little information available on the mechanisms driving the changes in the number of wintering birds. This chapter therefore applies the methodology outlined in the first section of this thesis, with the construction of a population model with random inputs, and the analysis of possible shooting strategies using the distribution of persistence times as a population viability measure.

The data relating to the Islay wintering barnacle geese consists, to a large extent, of the November census data and the counts of the proportion of young in the flocks (Table 7.1). By contrast, the smaller Svalbard breeding barnacle goose population has been extensively studied through the used of ringing to identify individuals (see, for instance, Owen & Black, 1989, who consider the lifetime reproductive output of individuals in the Svalbard population). However, the differences in dynamics and behaviour of the three main barnacle goose populations (some of which are discussed by Percival, 1991, and Cabot & West, 1983) suggest that it would not be very useful to attempt to apply results of the Svalbard population in the modelling of the east Greenland breeding population.

A simple model

Attempting to build a complex model which incorporates as much detail as is known, or supposed, about the dynamics of the Islay wintering barnacle geese would inevitably result in a situation where the parameters of the model could take such a wide range of values that the results obtained would probably have minimal value. Consider instead the simple model

$$N_{t+1} = b_t N_t + S_t N_t \qquad [7.1]$$

where N_t is the number of female barnacle geese counted on Islay in the autumn of year t, S_t is the probability that a female survives and returns the following winter, and b_t represents the number of female young arriving on Islay in year t+1 per female present at the start of the winter of year t. The parameters b_t and S_t are calculated from the November count data of Table 7.1 by application of the relations:

$$\begin{aligned} b_t &= y_{t+1} P_{t+1} / P_t \\ S_t &= P_{t+1} / P_t - b_t \end{aligned} \qquad [7.2]$$

Table 7.1. The November count data for the years 1960–91 (from Boyd 1968, Ogilvie 1983b, 92, and Nature Conservancy Council counts) with the number of geese shot under licence for winters beginning November 1982–89, from Brodie (1991). Recruitment, b_t, and survival, S_t, from eqns. [7.2], and growth rate, r_t, given by $\ln(P_{t+1}/P_t)$. Means and variances in parenthesis exclude years with survival rates greater than one.

November count data			Number			
Year	Count (P_t)	% young	shot	b_t	S_t	r_t
1960	4600	9.7		0.13	1.13	0.23
1961	5800	10.7		0.08	0.97	0.05
1962	6100	7.6				
1963		30.6				
1964	8300	7.5				
1965		11.2				
1966	8400	13.0		0.34	1.63	0.68
1967	16500	17.1		0.08	0.73	-0.22
1968	13300	9.5		0.22	0.86	0.07
1969	14300	20.0		0.20	0.82	0.01
1970	14500	19.4		0.16	0.99	0.14
1971	16600	13.6		0.13	0.92	0.04
1972	17300	12.1		0.18	0.86	0.05
1973	18100	17.4		0.14	0.93	0.07
1974	19400	13.0		0.14	0.90	0.04
1975	20200	13.9		0.27	0.92	0.17
1976	24000	22.4		0.04	0.78	-0.20
1977	19600	4.9		0.13	0.99	0.12
1978	22000	12.0		0.07	0.72	-0.24
1979	17300	8.3		0.14	1.05	0.17
1980	20500	11.4		0.05	0.67	-0.33
1981	14800	7.3		0.06	0.81	-0.15
1982	12800	6.7	956	0.13	1.14	0.24
1983	16217	9.9	731	0.14	0.92	0.06
1984	17213	13.4	447	0.11	0.93	0.04
1985	17875	10.7	541	0.19	1.04	0.21
1986	21970	15.5	791	0.12	0.87	0.00
1987	21900	12.5	505	0.11	0.82	-0.07
1988	20380	12.0	752	0.22	1.00	0.20
1989	24860	18.1	915	0.27	0.86	0.12
1990	28000	23.7		0.04	0.75	-0.24
1991	22000	4.7				
Mean				0.14 (0.134)	0.93 (0.864)	0.05 (-0.012)
Variance				0.01 (0.005)	0.03 (0.009)	0.04 (0.022)

where P_t is the total November population count in year t, and y_t the proportion of first winter birds in the flocks.

The model [7.1] is thus easily paramaterised from the available data. The relations [7.2] require the assumption of a constant, age-independent sex ratio. There is little available data to judge this assumption. The few catches of adult geese reported in the literature (e.g. Cabot *et al.* 1984) show no significant deviation from a 1:1 sex ratio. Studies of individually marked birds have shown a higher mortality rate in females in the Svalbard breeding population (Owen & Black 1989) but not in the Russian breeding population (Ebbinge, van Biezen & van der Voet 1991).

In the remainder of this chapter b_t will be referred to as recruitment and S_t as survival. The form of the model [7.1] essentially suggests that the barnacle geese wintering on Islay is a closed population. As was discussed in chapter 6, however, there is evidence that a minority of birds are mobile between wintering areas, both within a winter and between winters (Percival 1988, 1991; Newton & Percival 1989). These facts can be accommodated in the framework of the simple model presented here by recognising that some of the adult birds counted on Islay in November may, in fact, have spent the previous winter elsewhere and are, therefore, strictly immigrants to the Islay group rather than survivors from the previous winter, and that some young birds may be the offspring of females which did not spend the previous winter on Islay. The parameters termed "recruitment" and "survival", as calculated from [7.2], actually incorporate these other factors.

The presence of birds on Islay during a November count one winter, that wintered in areas other than Islay in previous years, may be one reason why "impossible" survival values greater than one arise on occasions (Table 7.1). Another reason may of course be counting errors. Ebbinge, van Biezen & van der Voet (1991) point out that if an abnormally large proportion of birds are missed in one November count, but not the next, the presence of a given count in the numerator of the survival estimates one year and the denominator the next, will lead to an underestimated survival rate followed by an overestimate. They found, however, that the mean survival value determined by estimates of the proportion of young in flocks compared favourably with estimates based on resightings of ringed individuals.

Recruitment, as given by b_t in eqn. [7.2], differs from the definition of recruitment used in the previous chapter. There recruitment was based on the number of young estimated to be present on Islay in one winter per adult present the previous winter that could be classified as a potential breeding bird. It was assumed that the age of first breeding was three years. To calculate this "age-structured" recruitment necessitated the assumption that survivorship was constant for all ages. This delay before first reproduction is not incorporated in the model of [7.1]. This omission is not as unfortunate as it may seem at first. Fig 7.1 demonstrates that there is, in fact, an almost linear relationship between the age-structured recruitment considered in chapter 6, and recruitment as defined here (eqn. [7.2]).

The structured recruitment of [6.3] is, of course, slightly larger than the *per capita* recruitment here as [7.2] attributes the same number of young birds to more females. In the absence of information on differential mortality attributable to age the relationship of Fig. 7.1 suggests that the use of a structured model will be of little value. The evidence from observations of the number of pairs that are accompanied by broods on the wintering grounds (Cabot & West 1983; Fox & Gitay 1991), and of direct observations of breeding success in Greenland (Cabot *et al.* 1984), is that the young present on the wintering grounds are actually the offspring of a rather small proportion of the breeding population, with many birds of a breeding age actually failing to successfully rear any young in a given year.

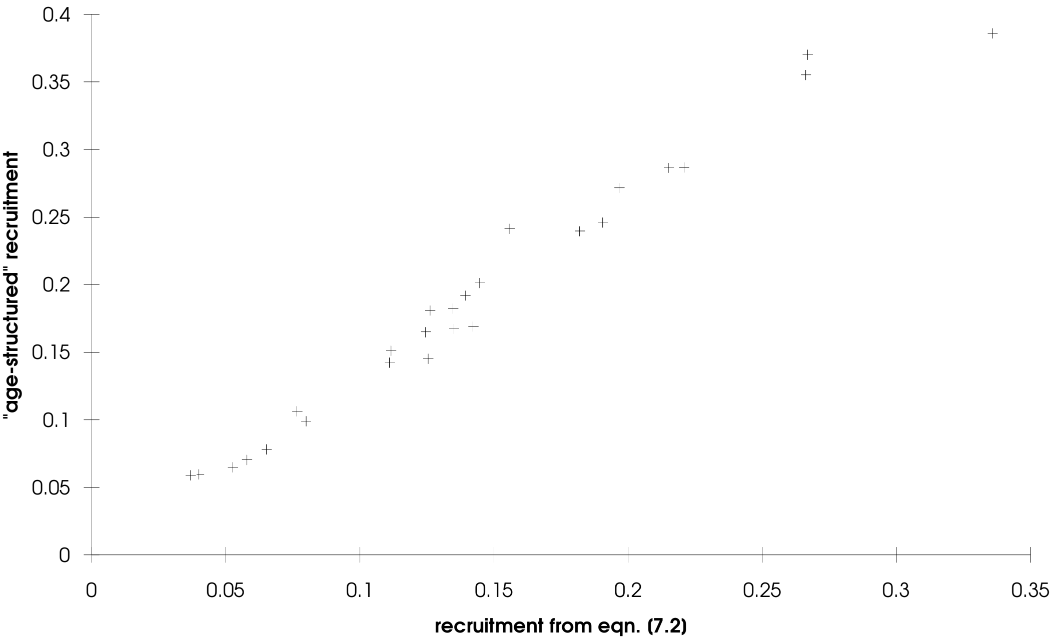


Figure 7.1. The relationship between the age-structured recruitment of chapter 6 (eqn. [6.3]) and the unstructured recruitment of [7.2].

In common with the recruitment and survival estimates discussed in chapter 6, b_t and S_t here (Table 7.1) show no obvious relationship with population size.

Persistence time with current vital rates

The simple model considered here, eqn. [7.1], to represent the dynamics of the Islay wintering barnacle geese from the November count data is, of course, just a special case of the simple multiplicative model of chapter 3. Here, the multiplicative growth rate, λ_t, is equal to $b_t + S_t$. The long run population growth rate, μ, and its variance σ^2, are estimated by the mean and variance of the logarithmic growth rate r_t, calculated in Table 7.1. So μ is estimated as 0.05 and σ^2 as 0.04. The long run growth rate thus supports the observed upwards trend in population size. Note that the formulae [3.6], which were used to approximate the long run growth rate and its variance from information on the multiplicative growth rate in the first section of this thesis, give very acceptable estimates of μ and σ^2 of 0.050 and 0.034 respectively.

However, a rather different situation emerges if the few years with "impossibly" high survival rates are excluded from the calculation of the mean and variance of the logarithmic growth rate. In this case μ is estimated as -0.012 and σ^2 as 0.022; in other words, there is a slightly negative long term growth rate. As discussed above either counting errors or immigration could have led to the survival rates greater than one, and the positive growth rate obtained earlier is doubtless the most representative of the data series. What this exercise demonstrates, however, is the importance of a few "good" years in producing the positive population growth rate over the last three decades. If population limiting mechanisms, such as a shortage of the better breeding sites in Greenland, are beginning to take effect then a long run growth rate around zero may be in prospect. In much of the following analysis two situations will be considered: (a) persistence time with the 'best estimate' from the data of a growth rate of 0.05, and (b) persistence time when the long run growth rate is around zero. The latter situation is included to give an indication of likely persistence times under a rather more pessimistic view of likely population growth rates.

From the analyses of chapter 3 it is apparent that, particularly where long run growth rates are positive, persistence time results depend on the level at which the lower threshold is set. Current numbers of female barnacle geese on Islay are in the region of 11000 individuals (from counts in the winter 1991/2). It is probably reasonable to assume that many conservationists would be concerned were the number of females

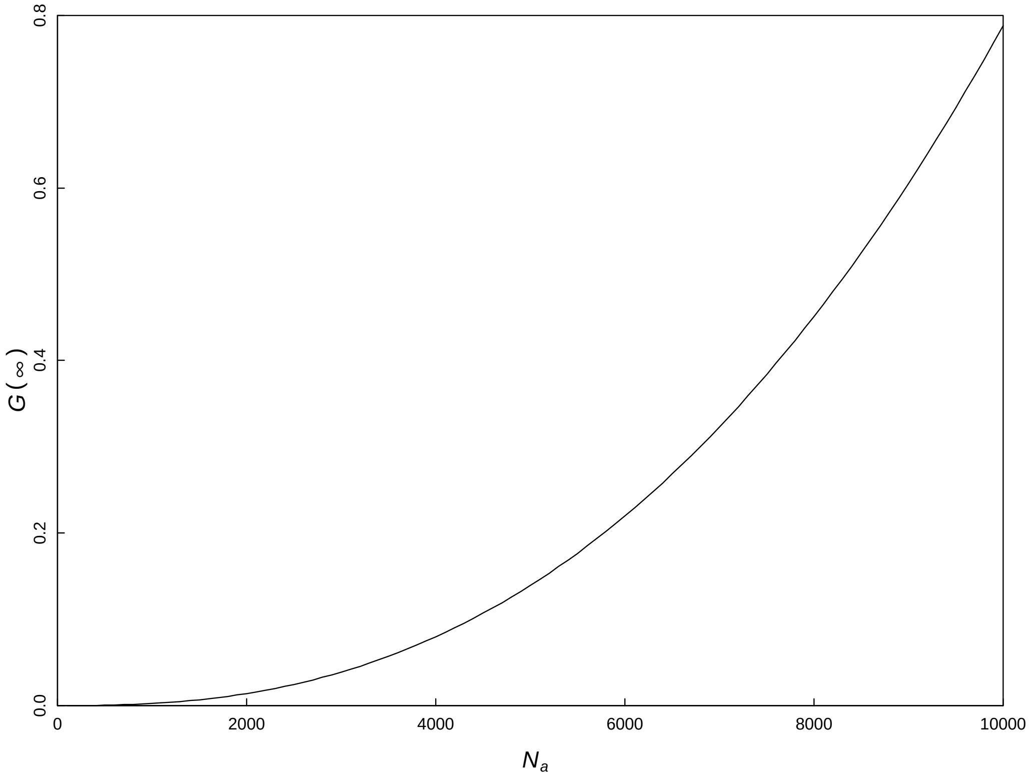


Figure 7.2. The probability, $G(\infty)$, of ultimately reaching the 'critical' lower population size, N_a, as this critical size is varied, calculated from [3.8]. $\mu = 0.05$, $\sigma^2 = 0.04$.

to drop to, say, 5000. Fig. 7.2 demonstrates the change in ultimate probability of reaching this level of concern, as the population size at which the level is set is varied. Thus, while the number of female barnacle geese wintering on Islay is quite likely to drop to 9000 or 10000 individuals, the probability of reaching a level of 5000 females is 0.139, given the observed positive growth rate. Of course, should the population growth rate be nearer zero, reaching a level of 5000 females is virtually certain (eqn. [3.13]).

Fig. 7.3 shows the probability density functions, calculated from eqn. [3.9], for persistence time under the two scenarios considered above. The two curves are similar in shape (because both sets of parameters give rise to fairly similar values of ϕ, the shape parameter discussed in chapter 3, eqn. [3.12]) but the area under the persistence time distribution for the positive growth rate, which was the best estimate of the population growth rate from the data of Table 7.1, is much smaller. This is, of course, a feature of the much reduced ultimate probability of reaching the threshold conferred by the positive growth rate. With a growth rate, μ, equal to 0.05 the

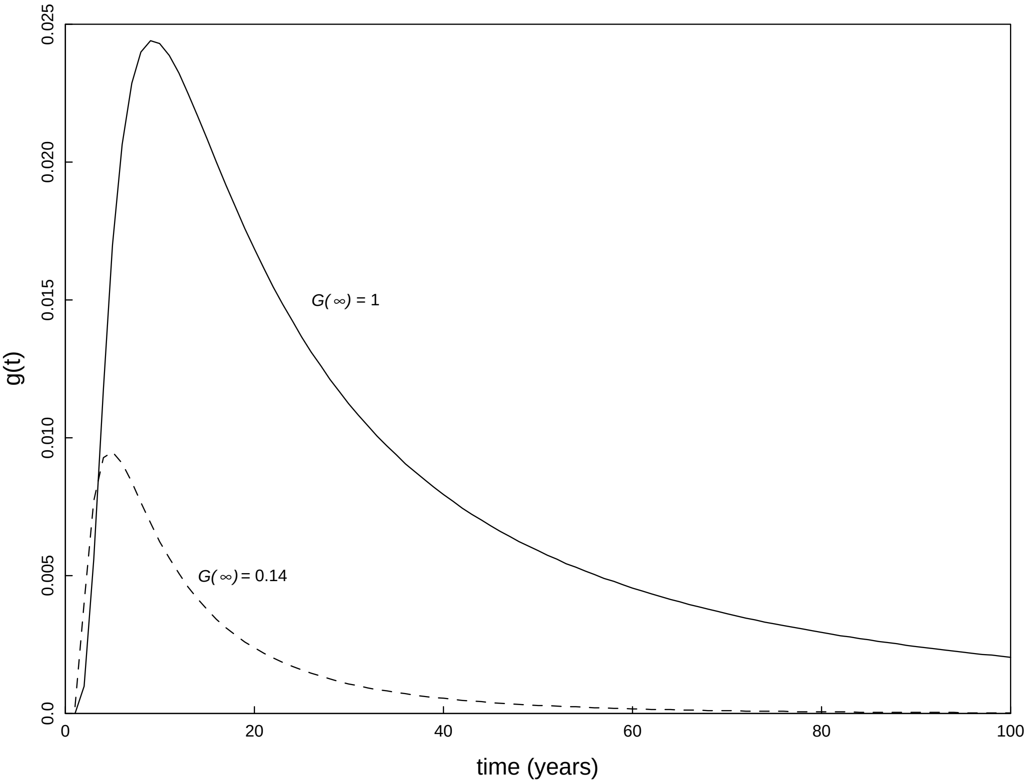


Figure 7.3. The persistence time distribution for the simple model [7.1], calculated from eqn. [3.9] with (– – –) μ = 0.05, σ^2= 0.04 (best estimate of population growth rate from data of Table 7.1: see text, p.170); (——) μ = –0.012, σ^2 = 0.022 (population growth rate calculated with survival rates greater than one excluded). N_0 = 11000, N_a = 5000. Ultimate probability of reaching the threshold, $G(\infty)$, calculated using [3.13].

greatest probability of reaching a level of 5000 females occurs in the next decade. If the population continues to grow at this rate then the probability of dropping to this small population size is much reduced. Where the growth rate is calculated with the exclusion of the few years with high survival rates, reaching a level of 5000 females is ultimately certain. The most likely persistence time is of the order of 10 years, but reasonably long persistence times could also arise.

The effects of autocorrelation in the recruitment rate

The analysis of chapter 6 suggests that there may be a tendency for some clustering of good or bad years in the rate of recruitment of juvenile birds. The simple model of chapter 3 considered only the case of serially independent fluctuations in the population growth rate. Tuljapurkar & Orzack (1980) suggest that, while the ultimate probability of reaching a lower threshold is not likely to be greatly affected by autocorrelation, the actual distribution of persistence times in a linear population model is likely to be quite sensitive to environmental autocorrelation.

The effect of autocorrelation in the recruitment rate on persistence time in the model [7.1] can be evaluated by calculating persistence times numerically, with the recruitment and survival rate given by

$$\begin{aligned} b_t &= (1-\alpha)\bar{b} + \alpha b_{t-1} + \sigma_Z Z_t \\ S_t &= \bar{S} + \sigma_S Y_t \end{aligned} \qquad [7.3]$$

where $\bar{b}$ and $\bar{S}$ are mean recruitment and survival rates, α is a measure of autocorrelation in recruitment rates, and Z_t, Y_t are Gaussian random variables with zero mean and unit variance.

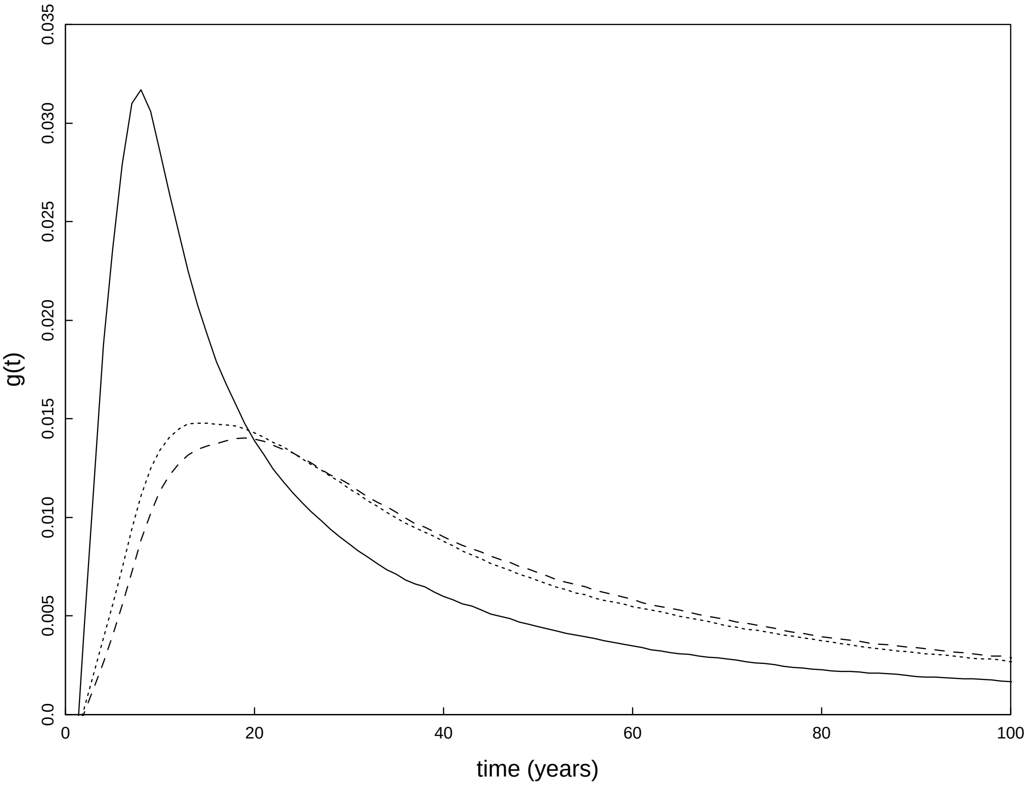


Figure 7.4. The effect of autocorrelation in recruitment rate on persistence time in the model [7.1] with recruitment and survival given by [7.3]. α = 0.8 (——), α = 0.2 (········), α = 0 (– – –). In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\bar{b}$ = 0.134, $\bar{S}$ = 0.864, σ_Z = 0.0707, σ_S = 0.0949. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

Fig. 7.4 demonstrates the effect on persistence time of different levels of autocorrelation in the recruitment rate when the 'driving' environmental variance, σ_Z, is fixed and the population is not growing. Such autocorrelation in general produces a reduction in persistence time, rather slight at lower levels of autocorrelation, but more marked as the autocorrelation is increased. Where the population is growing and autocorrelation is introduced into the birth rate (Fig. 7.5) the major effect is to increase the ultimate probability of reaching the threshold, especially when the autocorrelation is strong. In contrast to Fig. 7.4 there is no tendency for the modal persistence time to be reduced.

The autocorrelated rate of recruitment, b_t, as given by [7.3], is a first order

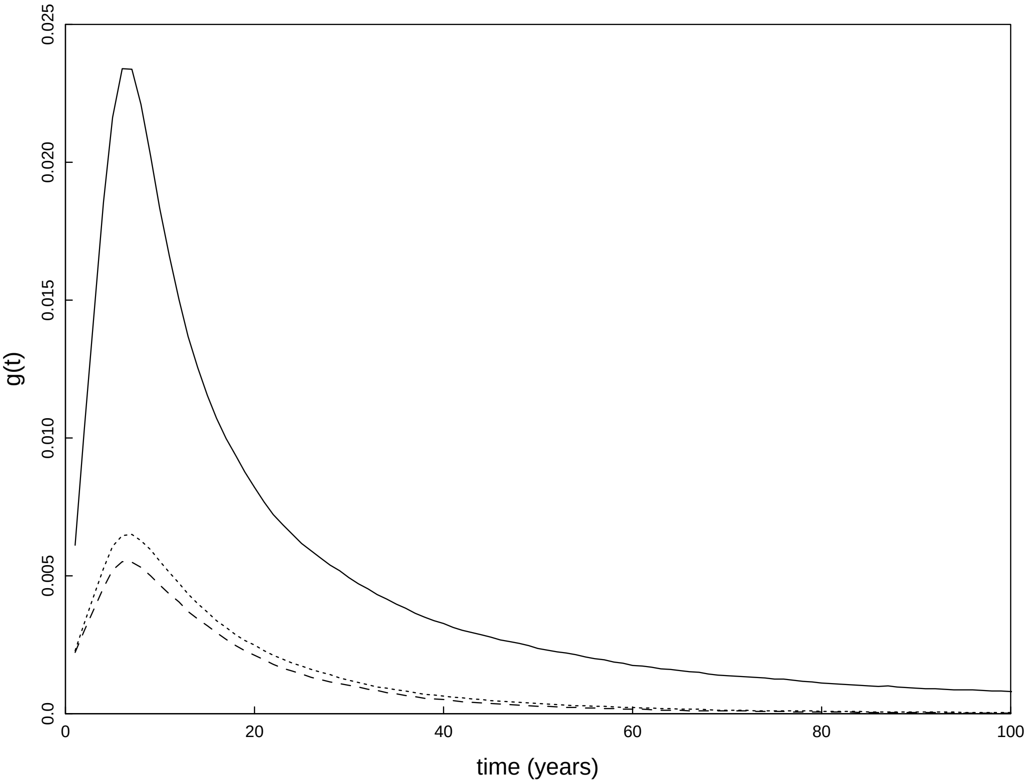


Figure 7.5. The effect of autocorrelation in recruitment rate on persistence time in the model [7.1] with recruitment and survival given by [7.3]. $\alpha = 0.8$ (——), $\alpha = 0.2$ (········), $\alpha = 0$ (– – –). In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\overline{b} = 0.14$, $\overline{S} = 0.93$, $\sigma_Z = 0.1$, $\sigma_S = 0.17$. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

autoregressive process. The variance in growth rate is, therefore, given by (Chatfield, 1984, p.45):

$$\sigma_b^2 = \frac{\sigma_Z^2}{\left(1-\alpha^2\right)} \qquad [7.4]$$

Increasing the degree of autocorrelation (α) thus increases the variance in recruitment rate. The decrease in persistence time noted in Fig. 7.4, and the decreased probability of persistence of Fig. 7.5, cannot, therefore, be attributed solely to the effects of autocorrelation: the increased variance in recruitment rate will also affect the persistence time distribution.

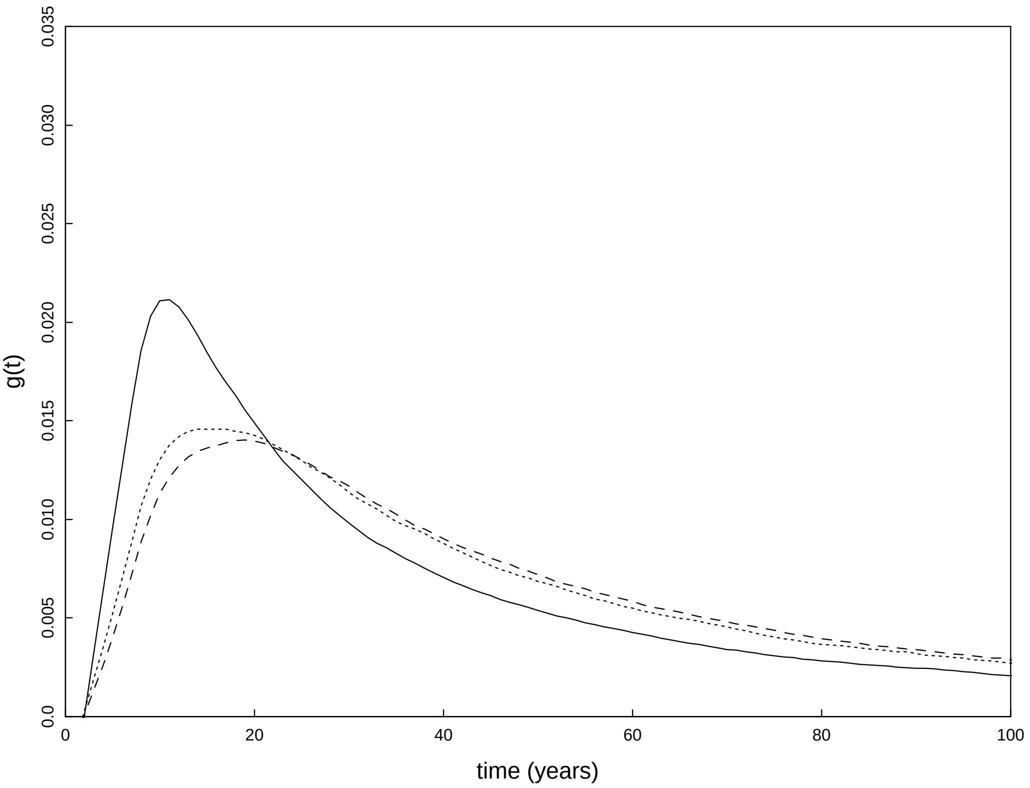


Figure 7.6. The effect of autocorrelation in recruitment rate on persistence time in the model [7.1] with recruitment and survival given by [7.3] and α chosen to give constant variance in recruitment rate. $\alpha = 0.8$, $\sigma_Z = 0.0424$ (——); $\alpha = 0.2$, $\sigma_Z = 0.0693$ (········); $\alpha = 0$, $\sigma_Z = 0.0707$ (– – –). In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\bar{b} = 0.134$, $\bar{S} = 0.864$, $\sigma_S = 0.0949$. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

To investigate the effects of autocorrelation alone on persistence time eqn. [7.4] can be used to choose values of σ_Z^2 such that the variance in recruitment rate, σ_b^2, is constant for different levels of autocorrelation, determined by α. This has been done in Fig. 7.6 which demonstrates that, where the population does not have a positive long term growth rate, autocorrelation alone still tends to reduce persistence time with the mode of the persistence time distributions under autocorrelation being at shorter times, and a higher probability of reaching the lower threshold, than the mode in the persistence time distribution without autocorrelation. The shift in the distribution towards shorter persistence times is, however, less marked than that observed in Fig. 7.4 where the environmental variance, σ_Z^2, was constant producing the confounding effect of increasing variance in recruitment with increasing autocorrelation.

For a growing population the effect of autocorrelation in the recruitment rate is again to increase the probability of reaching a lower threshold though the increase is not as great as that noted in Fig. 7.5 where the environmental variance, σ_Z^2, rather than the variance in recruitment rate, was constant.

The effects of shooting

To consider the effects of shooting the number, H_t, of female barnacle geese shot in the winter of year *t* is incorporated in the model [7.1] to give

$$N_{t+1} = b_t\left(N_t - cH_t\right) + S\left(N_t - H_t\right) \qquad [7.5]$$

Male and female geese are likely to be equally vulnerable to shooting. The total number of geese shot in a winter is then $2H_t$. The parameter *c* (which can take values between 1 and 2) is necessary because some females will lose their mate to shooting and thus fail to breed the following summer. Birds losing their mate in this way are assumed to have re-paired no later than the second breeding season after the loss of their mate (if they survive).

The only effect of shooting incorporated in [7.5] is actual loss of birds. As noted in the previous chapter there is little evidence of a direct effect of shooting on breeding success. In addition no redistribution of geese to other parts of the wintering range as a result of shooting is included. Ogilvie (1983b) found no evidence of geese being driven from Islay by the increased shooting pressure in the late 1970's.

Different management regimes for the regulation of shooting result in different functional forms for H_t. If shooting is to reduce conflict between farming and conservation interests then controlled shooting must not only curtail population growth, but must seek to prevent the population becoming endangered. If the population growth rate were constant from year to year (i.e. making [7.1] a deterministic model) then this compromise could be specified by insisting that the functional form for H_t should produce a stable equilibrium size for N_t in [7.5]. On this basis shooting controlled in a manner that does not take account of population size, such as shooting a constant number or proportion of geese annually, can be rejected as a suitable management strategy (Nisbet 1989; Middleton, Nisbet & Kerr 1993). Two reasonably simple strategies for controlling shooting which have functional forms for H_t that produce a stable equilibrium in a model with constant vital rates are (Nisbet 1989; Middleton, Nisbet & Kerr 1993):

(i) shooting a fixed fraction, a, of the excess of females above some threshold, T

$$H_t = \begin{cases} a\left[N_t - T\right] & \text{if } N_t > T \\ 0 & \text{otherwise} \end{cases} \tag{7.6}$$

(ii) as (i) but based on the number of females counted in the previous winter

$$H_t = \begin{cases} a\left[N_{t-1} - T\right] & \text{if } N_{t-1} > T \\ 0 & \text{otherwise} \end{cases} \tag{7.7}$$

The strategy (ii) has the advantage that shooting levels for a particular winter could be decided on the basis of the population census in the previous winter. This contrasts with strategy (i) which relies on counts of the birds arriving at the beginning of winter to determine shooting levels for that same winter.

The criterion that a shooting strategy should produce a stable equilibrium in the model [7.5] when vital rates are constant enables totally unsuitable strategies to be rejected. However, further analysis, that takes account of the observed fluctuations in the recruitment and survival rates (Table 7.1), is required before it can be concluded that either of the strategies above are suitable for the observed situation where vital rates fluctuate a great deal. For this reason changes in the persistence time distribution under the shooting strategies [7.6] and [7.7] are considered.

Persistence time under controlled shooting

Analytic insights

The shooting strategies [7.6] and [7.7] stabilise the size of the population described by [7.5] because they impose a form of density dependent mortality in a model where the vital rates otherwise fluctuate independently of population size. The inclusion of a threshold in these strategies, below which no shooting takes place, suggests comparison with the model of chapter 4, where a hard upper bound to population size was imposed on a linear (i.e. density independent) population model. In particular, where the proportion, a, of females over the threshold which is shot is one, similarity to the model with a hard upper limit equivalent to the threshold, T, is likely to be high. The main difference between the model considered here and the model of chapter 4 arises from the fact that the model here is based on a November census which takes place between the summer breeding and the winter when the threshold is enforced by shooting. The November census is the variable on which the persistence time above the lower critical size is based. In the model of chapter 4 this variable could not exceed the upper threshold, N_b. Here, the threshold may be exceeded due to the temporal separation of breeding and shooting mortality. Thus, even with the proportion shot, a, equal to one the shooting threshold, T, differs to some extent from a hard upper bound to population size.

Fig. 7.7 compares numerical estimates of persistence time under strategy (i) where $a = 1$, with persistence time distributions calculated from eqn. [4.3] with the upper limit, N_b, equal to the shooting threshold, T. The approximation is tolerable given the differences in the models discussed above. The mode of the distributions calculated from [4.3] coincide with the modes of the numerically estimated distributions and the distributions are similarly skewed. However both distributions of the persistence time under shooting show a slightly bimodality which cannot be produced by [4.3].

While the parallels between the model where all females over some threshold population size are shot and the model with a hard upper limit of chapter 4 are interesting, and the approximation to the distribution of persistence times reasonable, it is unlikely that such a high value of a would ever occur in a conservation management situation. Rather more relevant is comparison with the situation considered in chapter 5 where a population is fluctuating around some mean value.

For the threshold shooting strategies [7.6] and [7.7] necessary and sufficient conditions for a positive equilibrium with constant recruitment, $\bar{b}$, and survival, $\bar{S}$, are (Nisbet 1989; Middleton, Nisbet & Kerr 1993):

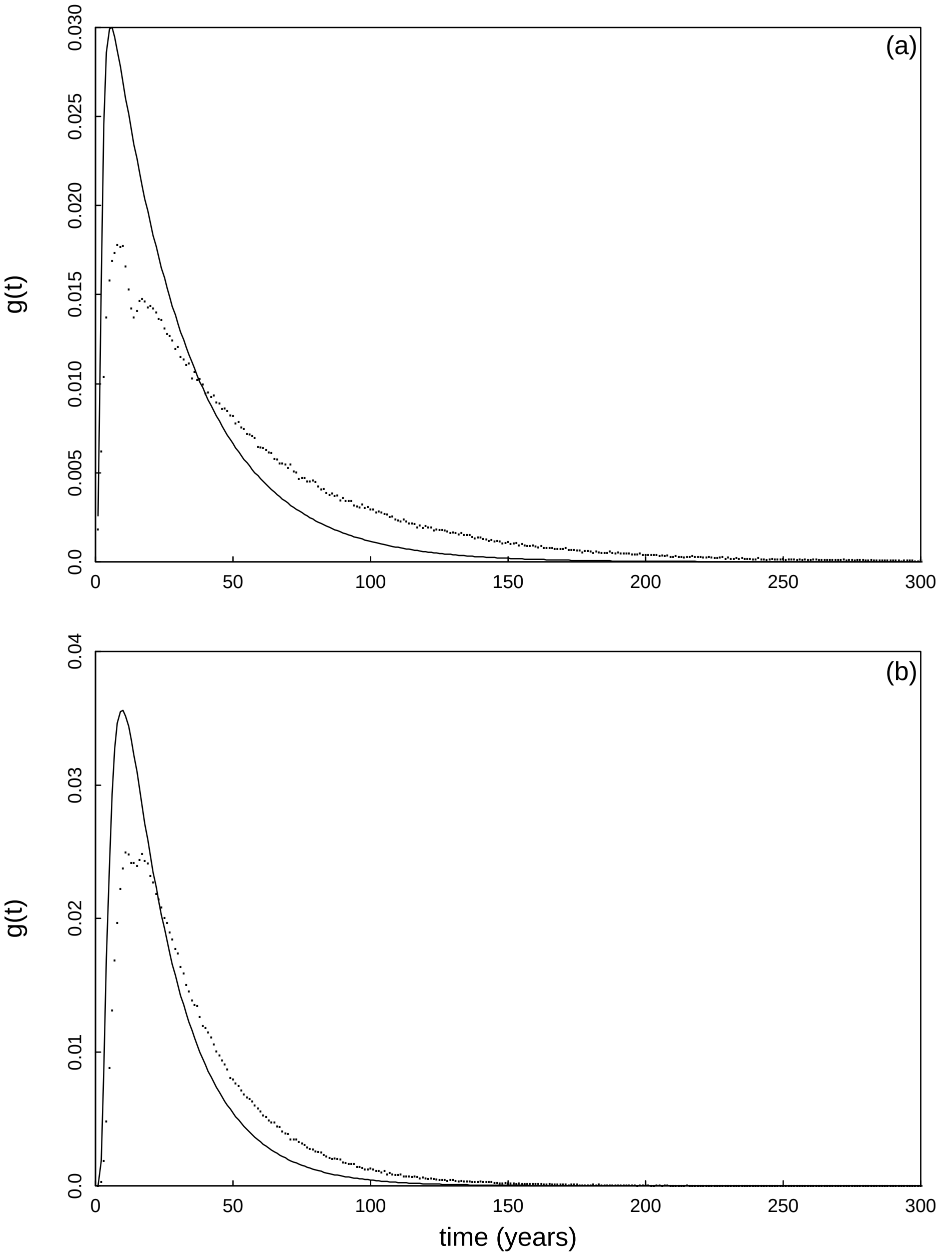


Figure 7.7. Comparison of (·····) numerically estimated persistence time distributions for the goose model with shooting regulated under strategy (i), with the proportion over the threshold shot equal to one, and (——) the linear model with a hard upper threshold where persistence time is given by [4.3]. (a) growing population: $\bar{b} = 0.14$, $\sigma_b = 0.1$, $\bar{S} = 0.93$, $\sigma_S = 0.17$; (b) no growth: $\bar{b} = 0.134$, $\sigma_b = 0.0707$, $\bar{S} = 0.864$, $\sigma_S = 0.0949$. $N_a = 5000$, $N_0 = 11000$, T (= N_h) = 10000 in both cases.

$$\begin{gathered}\bar{b}+\bar{S}>1\\ a<\left(\bar{b}+\bar{S}-1\right)\big/\left(\bar{b}c+\bar{S}\right)\end{gathered}\qquad [7.8]$$

For local stability shooting under [7.6] requires the condition

$$a<\left(1+\bar{b}+\bar{S}\right)\big/\left(\bar{b}c+\bar{S}\right)\qquad [7.9]$$

in addition to the inequalities [7.8] while strategy [7.7] requires the additional condition

$$a<1\big/\left(\bar{b}c+\bar{S}\right)\qquad [7.10]$$

Thus, if recruitment and survival were constant at their mean values (calculated from the data of Table 7.1) of 0.14 and 0.93 respectively, shooting under strategy (i) with $c = 2$, eqn. [7.6], would result in a stable equilibrium for $0.06 < a < 1.71$ whilst strategy (ii), eqn. [7.7], requires $0.06 < a < 0.83$. For the mean rates calculated with years with "impossible" survival rates excluded a positive equilibrium would not arise as $\bar{b} + \bar{S} < 1$.

With fluctuating recruitment and survival rates the population size may fluctuate around some mean value related to, but (as was the case in Roughgarden's model investigated in chapter 5) probably less than, the deterministic equilibrium population size. The existence of such a "stochastic equilibrium" is, of course, dependent on the level of variability in these rates. In particular the long run growth rate, μ, would require to be positive (replacing the condition for the deterministic case that $\bar{b}+\bar{S}>1$ is necessary). Some narrowing of the potential values for a would also be likely, though the extent to which this occurs depends on what level of fluctuation around the mean population size is considered "stable".

The results of chapter 5 for the persistence time of populations fluctuating around some mean value suggest that the persistence time distribution will be exponential for all but short times. Unfortunately a general method for calculating the mean persistence times in such situations was not forthcoming. Local linearisation of the deviation from the mean population size under the threshold shooting strategies produces an autoregressive process (appendix 2). While such approximations were found to produce 'ball park' estimates for mean persistence time for Roughgarden's (1975) logistic with random carrying capacity, Fig. A2.2 demonstrates that the observed variance in recruitment and survival places the Islay barnacle geese outwith the range where the local linearisation is likely to be useful. The approximation

[A2.7] underestimates the variance in population size when compared with simulations of the full model. In addition the mean population size is found to be less than the deterministic equilibrium when vital rates are constant. In the next section the effect of shooting on persistence time is therefore investigated with the aid of numerically estimated persistence time distributions.

Numerical analysis

Persistence time distributions for the model [7.5] with shooting given by [7.6] or [7.7] can be estimated numerically with recruitment and survival given by

$$\begin{aligned} b_t &= \overline{b} + \sigma_b Z_t \\ S_t &= \overline{S} + \sigma_S Y_t \end{aligned} \qquad [7.8]$$

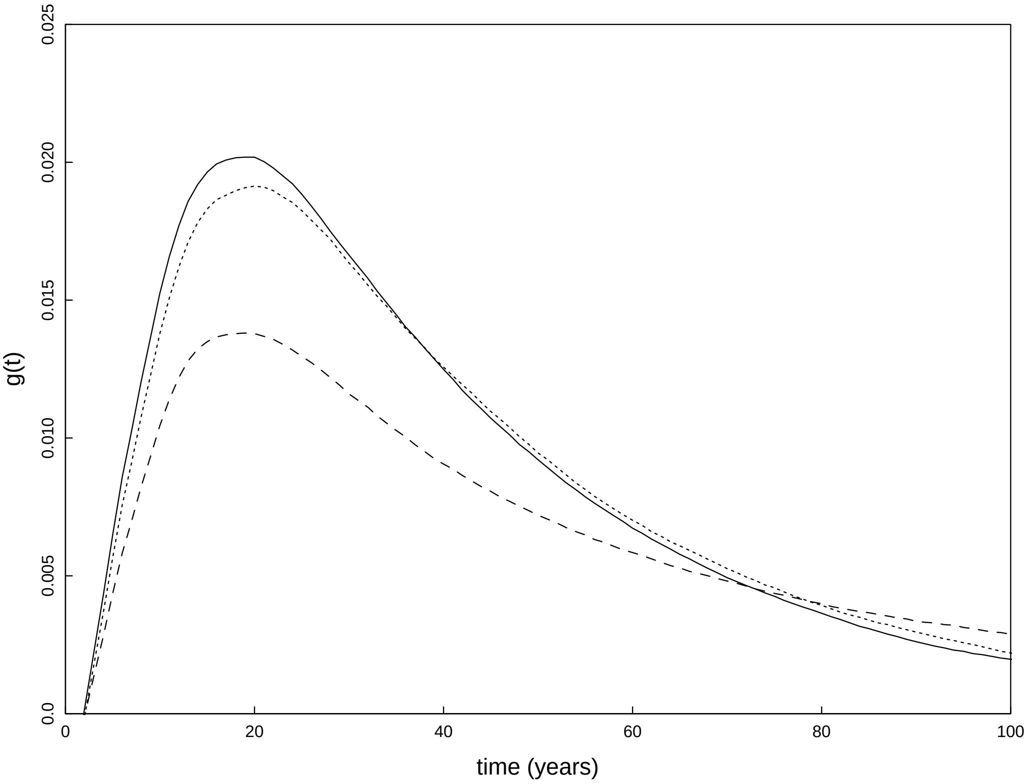


Figure 7.8. Numerical estimates of persistence time distributions for the model [7.5] with (– – –) no shooting; (········) shooting under strategy (i), [7.6], with *a* = 0.2, *T* = 10000, *c* = 2; (——) shooting under strategy (ii), [7.7], with *a* = 0.2, *T* = 10000, *c* = 2. In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\overline{b}$ = 0.134, $\overline{S}$ = 0.864, σ_b = 0.0707, σ_S = 0.0949. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 10 time steps.

where Z_t and Y_t are independent, Gaussian, random variables with mean zero and unit variance.

Figs. 7.8 and 7.9 illustrate the effect of shooting regulated under strategies [7.6] and [7.7] on the distribution of persistence times. For a slightly negative long run population growth rate (Fig. 7.8) the main effect of shooting under either strategy is to raise the probability of the population reaching the lower 'critical size' of 5000 individuals at short times. Because the ultimate probability of reaching the lower threshold is one in all three cases there is a corresponding reduction in the probability of reaching the threshold at longer times. The important point, however, is that the mode of the persistence time is not shifted to a shorter time by the imposition of shooting.

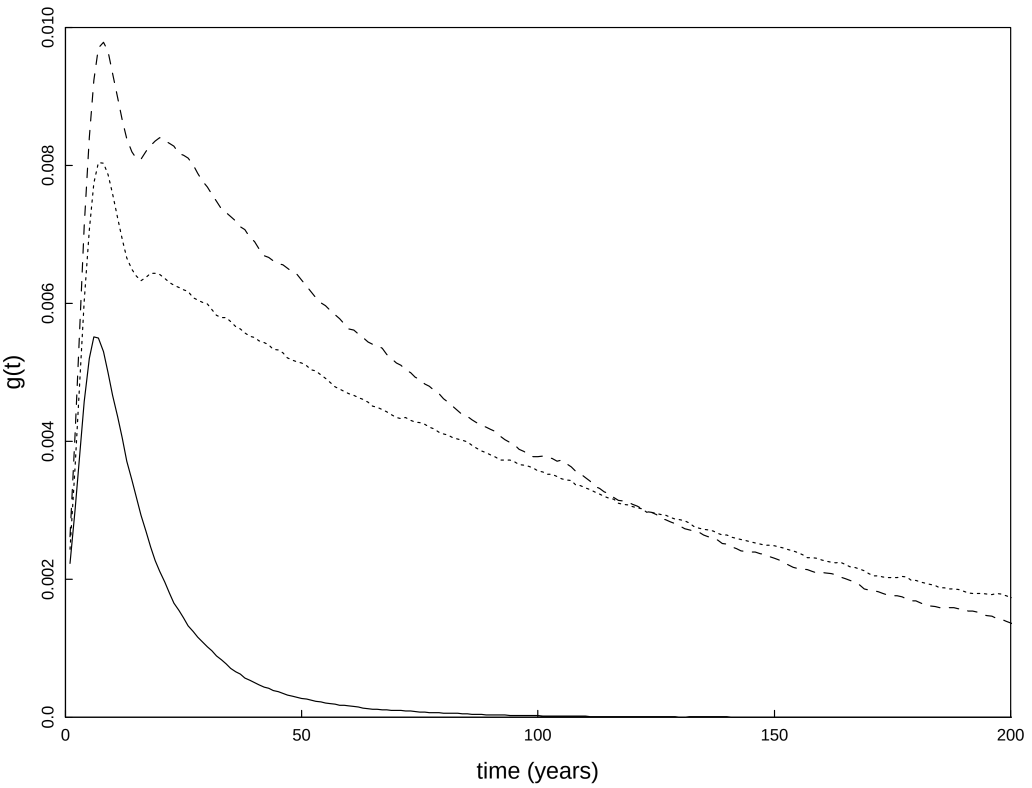


Figure 7.9. Numerical estimates of persistence time distributions for the model [7.5] with (——) no shooting; (·······) shooting under strategy (i), [7.6], with a = 0.2, T = 10000, c = 2; (– – –) shooting under strategy (ii), [7.7], with a = 0.2, T = 10000, c = 2. In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\overline{b}$ = 0.14, $\overline{S}$ = 0.93, σ_b = 0.1, σ_S = 0.17. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

For a population growth rate equivalent to the "best estimate" from the data of Table 7.1 there is a similar increase in probability of reaching the threshold at short times when shooting is imposed (Fig. 7.9), and again the modal persistence time is approximately the same as the no shooting case. However, the dominant feature of the persistence time distributions under shooting is the raised distribution tail. In this case shooting considerably increases the ultimate probability of the population reaching the lower threshold: this is due to the fact that the unconstrained population growth that was possible with a positive growth rate, and no (natural or imposed) regulation, is now prevented. The tail of the distribution is exponential, in line with the analyses of chapter 5 where an exponential persistence time distribution arose in models where the population was regulated around some mean size. The persistence

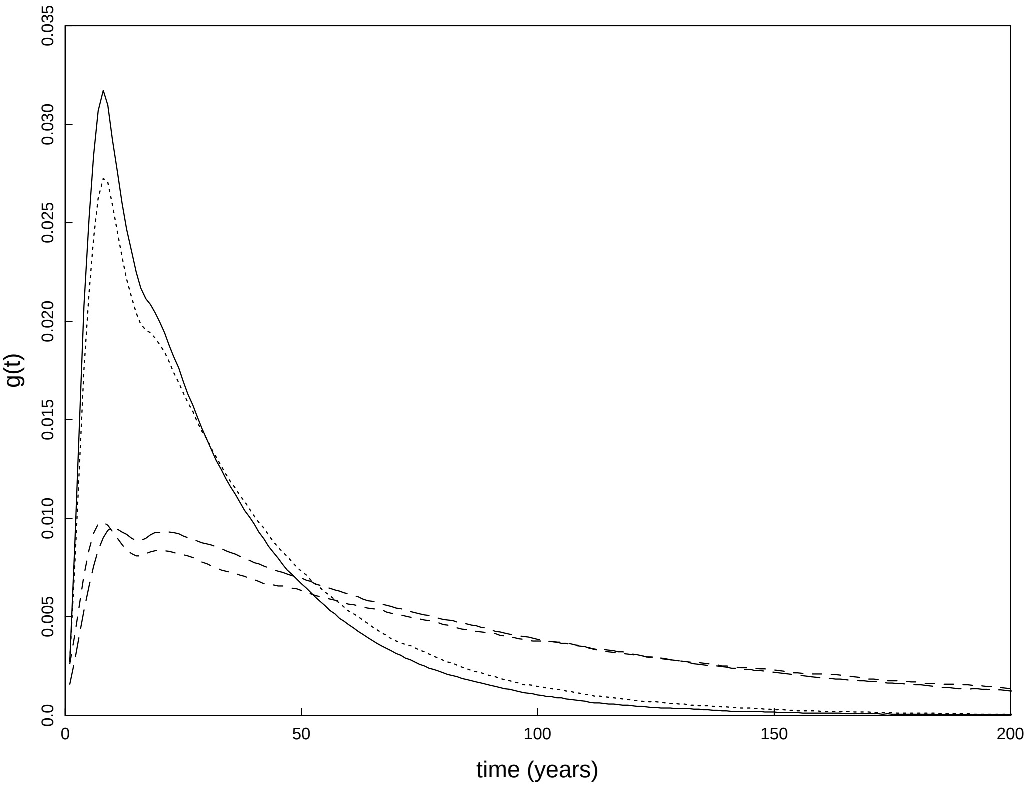


Figure 7.10. Persistence time distributions for the model [7.5] with shooting regulation based on the number of females in the previous winter, eqn. [7.7]. —— : $a = 0.6$, $T = 10000$, $c = 2$; ········ : $a = 0.6$, $T = 10000$, $c = 1$; — — : $a = 0.6$, $T = 15000$, $c = 2$; – – – : $a = 0.2$, $T = 10000$, $c = 2$. In all cases $N_0 = 11000$, $N_a = 5000$, $\bar{b} = 0.14$, $\bar{S} = 0.93$, $\sigma_b = 0.1$, $\sigma_S = 0.17$. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

time distributions under shooting also show a bimodality similar to that exhibited by Roughgarden's (1975) stochastic logistic, one of the models investigated in chapter 5.

Fig. 7.10 shows persistence time distributions for different values of *a* (the proportion shot), *T* (the threshold number of females, below which no shooting is allowed), and *c* (the effect of mate loss on recruitment). In all cases the modes of the distributions are similar to that of the persistence time distribution without shooting. The main effect of a change in parameters is in the probability of reaching the threshold at a given time. For a threshold level, *T*, an increase in the proportion of females over the threshold shot results in an increased probability of reaching the small population size of interest, N_a, at short times (balanced by a decreased probability at longer times). Decreasing the value of *c* (i.e. assuming that a greater proportion of the females whose mates are shot form new pairings before the summer) results in a slightly decreased probability of reaching the 'critical' level at short times (the first two decades from the imposition of controlled shooting).

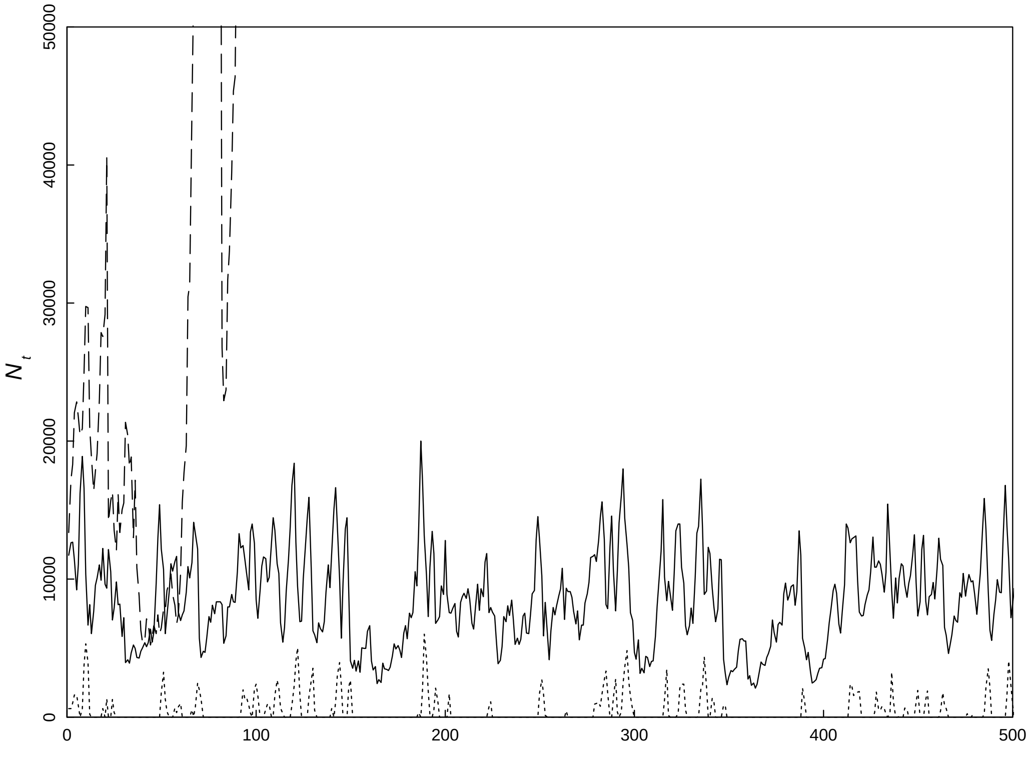


Figure 7.11. Realisations of the model [7.5] with N_0 = 11000, $\bar{b}$ = 0.14, $\bar{S}$ = 0.93, σ_b = 0.1, σ_S = 0.17. – – – : number of females with no shooting. —— : number of females (and ········ number of females shot) with shooting regulated by [7.7] with *a* = 0.6, *T* = 10000, *c* = 2.

Setting the shooting threshold at a higher number of females, for a given value of *a*, reduces the probability of dropping to the critical level at short times. In general increasing the impact of shooting (by increasing *a* or lowering *T*) does not greatly change the most likely persistence time, rather it results in a narrowing of the persistence time distribution such that long persistence times become less likely.

Fig. 7.11 shows realisations of the model [7.5] with and without shooting for the 'best estimate' recruitment and survival rates of Table 7.1. Without shooting the positive long run growth rate of 0.05 means that the population, despite fluctuating a great deal, rapidly grows beyond the scale of the figure. By contrast, the population with shooting regulated by strategy [7.7] is prevented from growing and remains fluctuating around a moderate level. The value of the parameter *a* in the threshold shooting strategies [7.6] and [7.6] determines the extent to which the number of females can fluctuate to high levels. Shooting has much less effect on the lower limit to which the population fluctuates. Because shooting ceases when the number of females falls below the threshold level the lower limit is largely a product of the variance in the population growth rate. By restricting the upper limit of population size, shooting means that a poor run of growth rates will bring the population to the lower limit (which is also, for the same reason, slightly lower as a result of shooting) more often. It is this effect which results in the higher probability of reaching a low population size at short times.

The effects of autocorrelation in the recruitment rate

It was demonstrated above that autocorrelation in the rate of recruitment tended to increase the probability of reaching the lower population size of interest at shorter times. It is important to consider whether this effect is accentuated under shooting, in particular where there are lags in the regulation imposed by shooting, as in strategy (ii), eqn. [7.7]. Fig. 7.12 shows the effect of shooting, where the number shot is based on the number of females in the previous winter, eqn. [7.7]) for simulations with the same parameters as Fig. 7.4. In all cases the imposition of shooting raises the probability of reaching the lower population size of interest at shorter times. However, there is little evidence that the shooting interacts with the autocorrelated recruitment rate to reduce persistence times beyond that of the independent effects of autocorrelation and shooting.

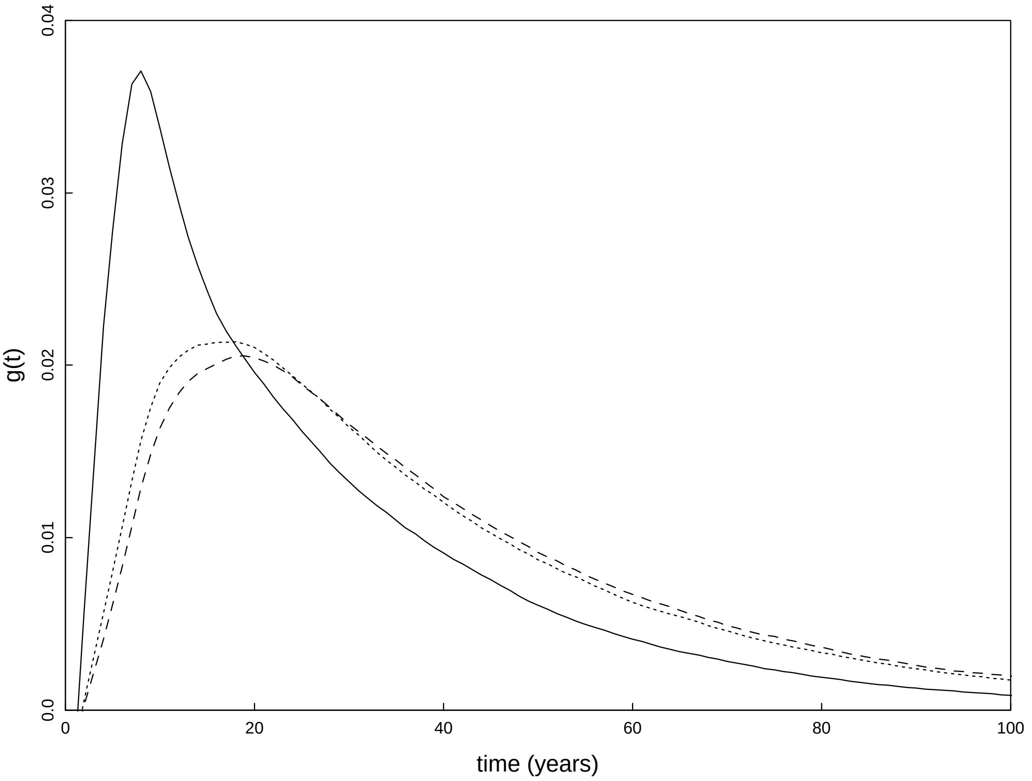


Figure 7.12. The effect of autocorrelation in recruitment rate on persistence time distributions for the model [7.5] with shooting regulated by [7.7]. $\alpha = 0.8$ (——), $\alpha = 0.2$ (········), $\alpha = 0$ (– – –). In all cases the initial number of females, N_0, is 11000; the lower threshold, N_a, is 5000 females, $\overline{b} = 0.134$, $\overline{S} = 0.864$, $\sigma_Z = 0.0707$, $\sigma_S = 0.0949$, $a = 0.2$, $T = 10000$, $c = 2$. Persistence time distributions were estimated numerically and smoothed using a symmetric nearest neighbour linear least squares procedure with a span of 5 time steps.

Discussion

It is apparent from the analysis above that shooting, controlled under a strategy such as [7.6] or [7.7] which imposes a form of density dependent mortality on the population, could effectively regulate the numbers of barnacle geese wintering on Islay (i.e. prevent future increases in population size due either to long term positive growth, or 'chance' fluctuations to larger sizes in a population with a growth rate near zero) without reducing the most likely persistence time above some lower 'critical' population size. For the population growth rate of 0.05, estimated from the data of Table 7.1, the imposition of shooting controlled under a threshold strategy results in an increase in the ultimate probability of the population dropping to the small size of interest. This is due to the fact that populations are prevented from growing without limit, a situation which the model [7.1] admits in the absence of shooting. It could be argued that this possibility is unrealistic and that the increase in the ultimate probability of reaching a small population size when shooting is imposed is thus overestimated (in other words, the 'true' probability of fluctuations to a low size in the absence of shooting is greater).

An important question that remains is to judge what the effect of imposing shooting on a naturally regulated population would be. If natural population regulation is currently active in the Islay barnacle goose population but undetected by the analyses of the previous chapter, or perhaps would occur if the population were to grow much more, would the imposition of the threshold shooting strategies [7.6] or [7.7] have a deleterious effect on population persistence undetected by the foregoing analysis ? The results of chapter 5 suggest that if natural density dependence were to act to regulate the population around some mean size then the most noticeable effects on the persistence time distribution would probably be at longer times, producing a distribution with an exponential tail, rather similar to the effect of imposed regulation demonstrated in Fig. 7.9. Natural density dependence may result in a raised ultimate probability of dropping to a small population size relative to the linear model, as growth to extremely large population sizes would be prevented. If the form of natural population regulation was such that population growth was enhanced at especially small population sizes then this could have a major effect on the lower limit to population size, reducing the probability of reaching the critical level. The effect of controlled shooting on a naturally regulated population is thus likely to further regulate fluctuations to larger population sizes, but unlikely to have any effect on persistence time other than a slightly increased probability of reaching the lower threshold.

While the modelling exercise carried out in this chapter suggests that shooting regulated in such a manner that it imposes a form of density dependent regulation on the Islay barnacle goose population may well be a satisfactory method of regulating population size (thus preventing increased conflict with agricultural interests) without greatly affecting the likely persistence time of the population, this result must be considered in the light of relevant legislation, public opinion, and practicality. While modelling can assess the affects of management on a populations dynamics it can say virtually nothing about the moral perspective of culling an internationally protected species !

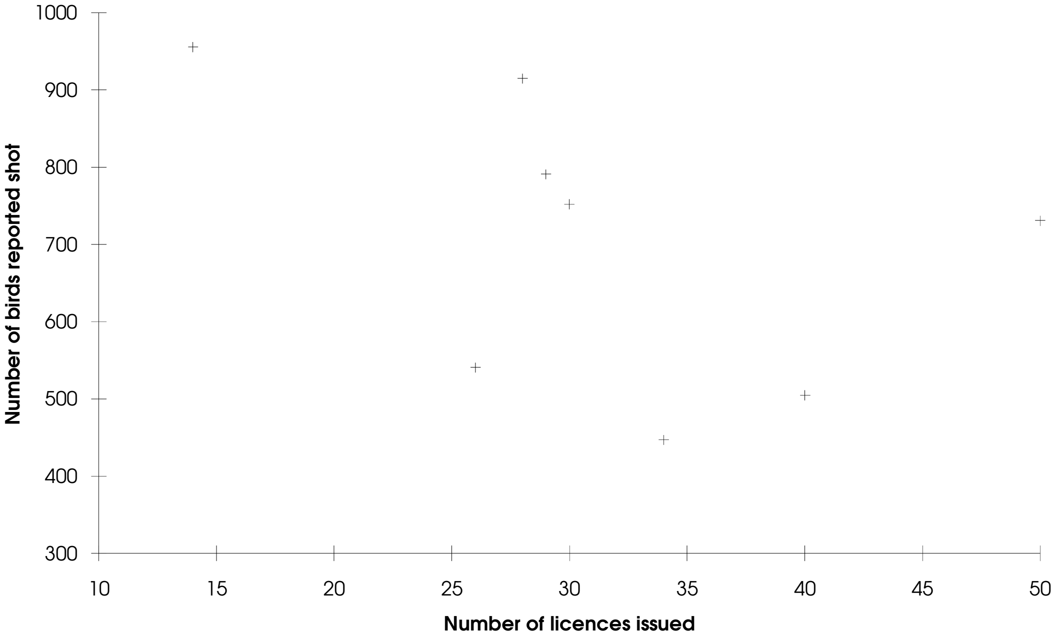


Figure 7.13. The relationship between the number of licences issued by DAFS for shooting barnacle geese on Islay in the winters 1982/3 to 1989/90, and the number of geese reported shot. Data from Brodie (1991).

From a (possibly naive) legal perspective a strategy of controlled shooting may be permissible under the provisions of shooting to prevent agricultural damage. However the current licence system is unlikely to be of much use in its implementation. Brodie (1991) points out that there is no relationship between number of licences issued and the number of geese reported shot (Fig. 7.13). Further, restricting shooting to those issued with licences of the type currently issued would restrict shooting to areas outwith SSSIs. The model [7.5] assumes that shooting is spread uniformly across the population. Given that the Islay wintering barnacle goose population is known to be made up of groups faithful to different feeding sites on the island (Percival 1988,91), restricting shooting to part of the wintering population could have adverse consequences not detected in the analysis of this chapter.

Administering the shooting strategy through the provision of sport shooting would not currently be legal under either UK or European legislation. Owen (1990a) suggests that wildfowlers would not be want to be associated with any culling strategy, a view confirmed by Harradine (1991). Owen also suggests that increased shooting would attract considerable public outcry. However, it is interesting to note that the mean number of female geese shot in the simulation of Fig. 7.11 was only 488. Doubling this gives an estimate of the mean annual kill of both male and female geese. This figure, in the region of 1000, birds is not an especially great increase on the mean number reported shot under licence in the winters 1982/3 to 1989/90 of 705 (Table 7.1, data from Brodie 1991), though relating the number shot to the population size means that in some years the number shot will be much higher than this mean. Shooting is also likely to be more widely acceptable as a population management tool than other culling methods such as trapping or poisoning (either on the wintering or breeding grounds), as it is already widely accepted as a sport (Boere 1990).

It is possible that the provisions of the recent Scottish Natural Heritage Act which removes the 'two tier' compensation system on Islay, by allowing for payments to farmers outwith SSSIs suffering damage by goose grazing, will silence calls for culling of the wintering barnacle geese in the immediate future. However, if the upward trend in population size of the last three decades continues, such calls will doubtless be heard again. Even if the Islay wintering barnacle geese begin to exhibit natural regulation of population size, either by factors operating on the breeding grounds in Greenland or saturation of the wintering grounds, the population is still likely to show large fluctuations in size as a result of the observed variance in recruitment and survival (Table 7.1). In such circumstances a policy of allowing a certain amount of shooting over a threshold level, while perhaps not contributing greatly to the reduction of agricultural damage, may nevertheless act to defuse conflict between agricultural and conservation interests.

Some conservationists frequently cite the fact that the population of barnacle geese is very small in global terms (Ogilvie 1983b; Owen 1990a; Fox *et al.* 1990; Fox & Gitay 1991) implying that continued increases in the population are only to be welcomed. However, it is a fact that some species are naturally much rarer than others. Much of the recent increase in barnacle goose numbers can be attributed to the impact of man on the environment through the agricultural improvements carried out on Islay. Some examples of the problems associated with single species conservation measures which can result in degradation of the wider ecosystem were discussed in chapter 1. Boere (1990) acknowledges that increases in the quantity of wildfowl is not necessarily positive in a wider ecological context. Whilst there is little evidence that the large numbers of barnacle geese on Islay currently pose a threat to naturally occurring species, independently of the loss of semi-natural habitat resulting from the taking of more land into agriculture, this may not be the case if numbers continue to grow. The effect of increased numbers of barnacle geese on the staging and breeding habitats should also receive some consideration. Perhaps it is time for the objective of conservation plans for the Islay wintering barnacle goose to be concerned with maintenance of the population (recognising that fluctuations in numbers arise naturally as a result of the dependence of population growth rate on weather conditions) rather than its continued growth.

The provision of sanctuary areas has so far been the major management policy for the conservation of the Islay wintering barnacle geese (Bignal, Stroud & Easterbee 1990; Owen 1977,90a). While this has been successful from the point of view of safeguarding the geese, it has not prevented conflict with agriculture. Indeed by increasing the quality of grassland in an attempt to attract birds that were actually faithful areas elsewhere, it may only have served to increase both the population and the conflict. A future policy of population maintenance recognising the need to compensate farmers outwith sanctuary areas for having geese grazing on their land, and possibly allowing shooting at high population sizes (especially if the upwards trend in population size continues), may be more successful. Such a policy would preferably be part of an integrated conservation approach encompassing other species and habitats, rather than concentrating on a single species. Agricultural surpluses, and increasing potential for "natural heritage" to play a part in the economy of the highlands and islands of Scotland may make for an easier change to such a policy.

The Islay wintering barnacle geese are without doubt a national asset and must, as such, be protected. The part that agriculture on Islay plays in maintaining this asset is often, perhaps, underestimated. Like any asset, careful management is essential and in this case population modelling can help optimise the use of current knowledge in making management decisions.

Chapter 8

General discussion

This chapter is designed to give an overview of the results included in this thesis and to identify areas with potential for further work. Its purpose is not to repeat the discussions that are found at the end of each chapter but rather to present some general conclusions. Like the thesis, this chapter falls naturally into two sections: a discussion of persistence in simple population models, and a discussion of issues relating specifically to the Islay wintering barnacle geese.

Persistence time in simple population models

There is no doubt that persistence time is a useful measure of the behaviour of a stochastic population model. While persistence time was introduced in this thesis specifically in the context of population management, it also relates to issues in general ecological theory as the discussion of persistence and density dependence of chapter 3 demonstrated. The survey (chapter 2) of first passage time results available for simple stochastic processes demonstrated that the mathematics necessary for investigating the problem of persistence time is not very well developed, or especially accessible, at the current time. It is therefore very satisfying that, at least for persistence time in linear population models with independent environments, a fairly complete set of results exists, based on the first passage time of the Wiener process. The characteristics of persistence time in such models was extensively investigated in chapter 3. The most prominent omission from the current theory for persistence time in density independent models is a method for dealing with autocorrelated stochastic inputs. Turelli (1977) suggests that in many populations the underlying processes will in fact be subject to autocorrelated noise and that assuming independent environments is necessarily an approximation. Nisbet & Gurney (1982) suggest that "coloured" noise, with non-zero short term autocorrelation, is a more useful way of introducing stochasticity into population models than the uncorrelated white noise more often used. Lande & Orzack (1988) found that numerical estimates of persistence time in an age-structured model with density independent rates were approximated well by persistence time estimates based on the Wiener process first passage time distribution, if they accounted for the "built-in" autocorrelation introduced by age structure into their estimates of the long run growth rate and its variance. Numerical persistence time estimates for the model of Islay wintering barnacle geese considered in chapter 7 suggested that autocorrelated growth rates may have a substantial effect on persistence time. It would be interesting to investigate how well the persistence time distribution [3.9] approximates persistence time in an autocorrelated environment with appropriate adjustments in the mean and variance of the long run growth rate, despite the fact that the Wiener process (with its purely random inputs) can no longer be invoked as the limiting model.

In chapter 4 it was demonstrated that one unsatisfactory feature of most linear population models - the potential for unlimited growth resulting in unreasonably large population sizes - could be dealt with by the incorporation of a hard upper limit on population size. A biological mechanism giving rise to such a limit is competition for a finite and indivisible resource, such as breeding territories. Persistence time in such cases, where a linear model describes all changes in population size beneath this upper limit, can be found by considering the Wiener process with an upper reflecting barrier. The accurate expression for the first passage time of this process provided in chapter 2 allowed the thorough investigation of the properties of the persistence time distribution of this model in chapter 4. The advantage of having analytical results for persistence time in this model was demonstrated by the application to Stacey & Taper's (1992) Acorn Woodpecker data which discovered flaws in their numerical treatment.

While persistence time in models with density independent vital rates, and the useful extension to models with regulation through an upper limit to population size, is well characterised in chapters 3 and 4, persistence time in population models where the growth rate is density dependent remains unresolved in the general case. However some general insights are still possible. Non-linear stochastic population models where the population fluctuates around some constant mean size can be expected to give rise to an exponential distribution of persistence times for reasonably long times. For Roughgarden's discrete logistic with random carrying capacity, and the goose model of chapter 7 with threshold shooting, there is evidence of a bimodal distribution of persistence times, the second peak in the distribution marking the onset of the exponential portion of the distribution. Chapter 5 did not yield a general method for the mean persistence time based on this exponential distribution.

One difficulty of the two models considered in the first part of chapter 5, where it was possible to obtain expressions for the persistence time (or mean persistence time) by transformation to a simpler stochastic process, was the problem of differing interpretations of the stochastic differential equations. The "Ito-Stratanovich controversy" dogged stochastic population modelling for several years. Turelli (1977) suggested that, if any, the Ito calculus may be most appropriate for populations where the "true" underlying model can be considered to be a stochastic difference equation with autocorrelated noise. However, by its application of the rules of standard calculus, the transformation method of chapter 5 implied interpretation of the stochastic differential equations according to Stratanovich rules. Despite the fact that numerical estimates suggested that the two interpretations may lead to similar persistence time distributions for certain parameter combinations, it is well known that in some cases the different interpretations may lead to very different conclusions (Feldman & Roughgarden 1975, Turelli 1977). If a model is phrased in terms of stochastic differential equations it remains inherently ambiguous unless the appropriate calculus is also specified. It would be useful to find a model where persistence time could be investigated analytically for both Ito and Stratanovich interpretations. While this would necessarily be rather model specific, it may provide a qualitative feel for the effect of differing interpretations on persistence time.

Chapter 5 also investigated the use of local linearisation around a deterministic steady state as a means of approximating persistence time by utilising results for the Ornstein Uhlenbeck process. Where environmental variation is significant, and where the lower threshold of interest lies outwith the 'normal' range of fluctuations in population size (as will generally be the case in management situations), the persistence time distribution of the locally linear model may differ significantly from the distribution of persistence times in the full non-linear model. This results from the fact that the linear approximation underestimates the variance of the full model (though overestimation is also possible, e.g. Nisbet, Gurney, & Pettipher (1977)) and also that the actual mean population size in the stochastic model may be considerably less than the equilibrium size of the equivalent deterministic model, a feature which is especially important when persistence times are of interest. In addition to the problem of the linear model inadequately representing persistence time in the full non linear model, the results of chapter 5 also showed that the mean persistence time of the continuous time OU process generally underestimates mean persistence in the "corresponding", discrete time, autoregressive process. While persistence time results for the density independent models were insensitive to changes in time step, this is not the case in the density dependent situations considered here, a problem which must be considered in future investigations of persistence time in density dependent population models.

In summary then, a great deal of work remains to be done before insight into persistence time in density dependent population models reaches anywhere near the degree of completeness that exists for density independent models. In addition to considering general methods for persistence time in models with a constant mean population size, the problem of persistence time in cases where the corresponding deterministic model does not yield a stable point equilibrium (such as cyclic or chaotic models) must be considered.

One approach that may prove to be useful is that of Goodman (1987a,b). Goodman begins with the expression for expected persistence time in a birth and death process, then redefines the birth and death rates such that environmental variation (as well as demographic variation) can be incorporated. This gives an expression for mean persistence time which, in theory, could allow the incorporation of arbitrary forms of the dependence of growth rate on population size. If such a process proves to be generally valid then the resulting expression for mean persistence time, combined with the observation that populations fluctuating around a constant mean size show an exponential distribution of persistence times, could lead to more general insight.

The models considered in this thesis have all considered a spatially homogenous population affected by a temporally varying environment. An area that deserves attention is the affect of spatial (e.g. between patch) variability on population persistence. In chapter 3 it was suggested that a population subdivided into local populations affected by different temporal patterns of environmental variability could well have a much longer overall persistence time than any of its component subpopulations, if these were sufficiently connected that recolonisation took place after local extinction. A similar mechanism is also a possible explanation for the long persistence time observed in the Acorn Woodpecker population considered in chapter 4. Persistence time in both local and metapopulations will undoubtedly be the subject of much investigation in the near future as spatially variable populations are currently attracting a great deal of interest. Verboom, Lankester & Metz (1991), for instance, consider a stochastic metapopulation model for the badger (*Meles meles*). They find that a simple model with patches either in an occupied or empty state adequately describes a more complex model with detailed representation of local population processes. Fragmentation of suitable habitat is found to be especially important in persistence of the metapopulation: if suitable habitat is too widely spaced recolonisation does not happen frequently enough to compensate for the effects of local extinctions.

Population dynamics and management of the Islay barnacle geese

As a result of changes in the law to allow payments to farmers whose land attracts grazing geese but does not fall in a Site of Special Scientific Interest the conflict between agriculture and barnacle goose conservation on Islay at present is, apparently, not as acute as in previous years. However the overall trend in population size, despite the poor breeding success in the past two years, appears still to be one of increases in size. Unless natural population regulation is seen to be taking affect then the conflict with agriculture is likely to continue. The question of where population regulation will take effect needs to be considered. If the population is not currently limited by factors operating on the breeding grounds, such as shortage of suitable nesting areas, then continued agricultural improvements on Islay, together with increased refuge areas, and combined with the faithfulness of birds to particular feeding areas, are likely to lead to further increases in population size. If this is seen to happen, then consideration of the impact, not only on agriculture, but on the wider ecosystem may lead to the conclusion that some form of population limitation (possibly controlled shooting) is appropriate. Should this be the case then it is important that the shooting should be regulated in a manner that takes account of population size and that shooting is stopped when the population falls below some threshold size.

Understanding of the dynamics of the east Greenland breeding geese is fairly limited at present. The available data relates mostly to the Islay wintering birds, on which the models considered here were based, and to birds wintering on the Inishkea islands. Increased ringing and observation of marked birds in other parts of the wintering range is essential if understanding of the dynamics of the whole population (rather than just the Islay wintering portion) is to be advanced. However, as far as the situation on Islay is concerned, the most important area for study relates to the question of whether natural density dependence is beginning to act to limit population size. Given the problems of elucidating such information from simple census data, following the success of reasonably large numbers of individually marked birds is likely to be an important technique in this area also.

At the modelling level there is still opportunity for progress based on current knowledge and data. Of particular interest is the question of alternative management strategies. Protected areas, rather than controlled shooting, remain the current policy on Islay. Owen (1990a) suggests that a policy which sets up 'favoured areas' for geese, within which farming is oriented towards providing feeding for the geese and the geese are protected from disturbance, could be the model for protection of other geese populations wintering in Britain. Outwith these areas Owen suggests that shooting over agricultural land be permitted so long as the population does not fall below a certain level.

Models which incorporate favourable habitat surrounded by hostile areas have been used by biologists for some time (Gurney & Nisbet 1975, McMurtie 1978, Nisbet & Gurney 1982). The primary conclusion from these models is that dispersal mechanism and size of the favoured area may be as important as survival and recruitment in determining population viability. These models, however, generally consider random movement between areas, and simultaneous recruitment and death. Evaluating a policy of refuge provision in the case of the Islay barnacle geese necessitates considering several deviations from this simple model. This includes diurnal movement of the geese between feeding and roost sites (which may not both be in refuge areas), and within season movement between Islay and other wintering areas in the Inner Hebrides and Ireland. While, as discussed above, data on these matters is limited a modelling framework could be put in place and the policy evaluated in the light of current understanding of the population dynamics. Persistence time would be a useful measure of population viability in such efforts.

Appendix 1

Numerical estimation of persistence time distributions

This appendix briefly outlines the methods used in the numerical estimation of persistence time distributions. These methods were used both to confirm the analytic results presented in this thesis (and were thus instrumental in revealing the problems with published probability density functions for the Wiener process with an upper reflecting and lower absorbing barriers discussed in chapter 2) and also to estimate the persistence time distribution when the model of interest could not be cast in a form in which one of the first passage time distributions of chapter 2 could be applied.

Persistence time distributions were estimated by the "brute force" method of repeatedly iterating the difference equation describing the model, from a given initial state, and recording the time step at which the population size reached, or fell below, the lower threshold value of interest. The number of trials reaching the threshold at each time was then divided by the total number of trials to give an estimate of the probability of reaching the threshold at that time. Typically 300,000 to 500,000 trials were necessary to produce a persistence time distribution without too much variability in the probability of absorption at a given time (see Fig. A1.1).

The program was written along the same lines as other tools used by the mathematical biology group: the actual model for which the persistence time distribution was to be estimated being specified in a different file than the main program. This allowed different models to be specified with great ease. The program was initially implemented on a personal computer in Borland Turbo Pascal v.3. However the necessity of carrying out a great many trials in order to build up a clear picture of the persistence time distribution meant that this was not a viable platform, a single distribution taking several days to compute. The program was therefore rapidly ported to an Atari ATW transputer workstation and recoded in Prospero ProPascal. This provided the platform for computing simulated persistence time distributions for the first year of the project. The creation of the Department of Statistics and Modelling Science with extensive computing facilities enabled another change of computing environment, to Sun sparcstations and Sun Pascal. This enabled persistence time distributions to be computed in 10 to 15% of the time previously required. Without this computing power estimating persistence time distributions for continuous time models with euler integration would not have been possible.

The correct working of this program was tested by numerically estimating the first passage time distribution for the "Gambler's ruin" problem, for which the exact distribution is known. This problem considers a gambler, with initial capital £*z*, who loses or gains £1 each round with equal probability (½). The question is how long the game continues before the gambler is ruined (i.e. no capital remaining). This is, of course, equivalent to finding the first passage time of a simple, symmetric random walk to an absorbing barrier at zero. The probability at ruin at time (or round) *t* is given by (Feller 1968, eqn. III.7.5)

$$g(t) = \begin{cases} 2^{-n}\dfrac{z}{t}\dbinom{t}{\frac{1}{2}(t+z)} & \text{if } (t+z) \text{ is even} \\ 0 & \text{otherwise} \end{cases} \qquad \text{[A1.1]}$$

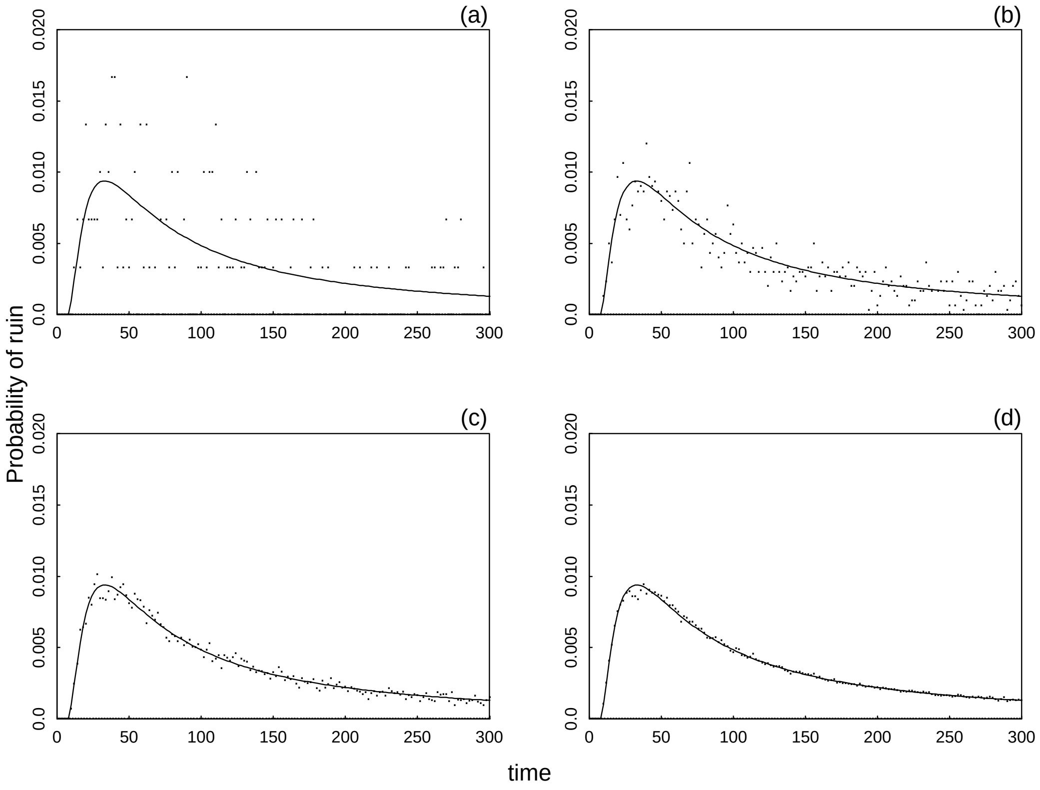


Figure A1.1. The first passage time for the classical gambler's ruin problem determined numerically by the methods described in this appendix, and compared with the exact formula [A1.1]. (a) 3.0E+2 trials, (b) 3.0E+3 trials, (c) 3.0E+4 trials, (d) 3.0E+5 trials. The initial capital, *z*, equals £10 in all cases.

Fig. A1.1 compares the distribution given by [A1.1] with that found numerically. This figure demonstrates both that the numerical method successfully estimates the first passage time distribution, and illustrates the earlier point about the large number of trials required to produce a distribution with as little variance as possible.

Euler integration of continuous time models

The program described here was constructed specifically to estimate persistence time in discrete time models described by difference equations with a time step of one. Persistence time for continuous time stochastic models could, however, be estimated by appropriately scaling the results to produce euler integration.

As an example consider the Wiener process with drift μ_W and variance σ_W^2. The first passage time distribution is estimated by euler integration of the generalised random walk

$$X_{t+1} = X_t + Z_t \qquad \text{[A1.2]}$$

where Z_t is a Gaussian random variable with mean μ_{RW} and variance σ_{RW}^2. To simulate the Wiener process with an integration time step of Δt [A1.2] is iterated with

$$\begin{aligned} \mu_{RW} &= \mu_W \Delta t \\ \sigma_{RW} &= \sigma_W \sqrt{\Delta t} \end{aligned} \qquad \text{[A1.3]}$$

The first passage time distribution obtained must then be scaled appropriately:

$$g_W(t) = \frac{g_{RW}(t/\Delta t)}{\Delta t} \qquad \text{[A1.4]}$$

Because a smaller time step is being considered there are more "opportunities" for a trial to reach the threshold in a given length of time. Thus for the same clarity of estimated persistence time distribution (i.e. similar variances in estimated probability of reaching the threshold at time *t*) as the $\Delta t = 1$ case the number of trials required is multiplied by $1/\Delta t$. Euler integration with a time step $\Delta t = 0.1$ thus increases the computation effort by an order of magnitude over the $\Delta t = 1$ case. As the number of trials required is large, even for the unit time step case, this is not a trivial increase and may require runs lasting several days even with the latest (sun) version of the program.

Random number generation

Uniform random deviates were produced using Sun Pascal's built in `random` function which appeared to perform as well as Press *et al.*'s (1989) `ran3` uniform random deviate generating function, as regards lack of serial correlation and uniformity of distribution. The built in function was generally preferred for reasons of speed When required Gaussian random deviates were produced from uniform random deviates by the transformation method (Press *et al.* 1989, function `gasdev`).

Appendix 2

Local approximation of the goose model with threshold regulated shooting

This appendix considers an approximation, in the neighbourhood of the deterministic equilibrium, to the goose model discussed in chapter 7 [7.5] with shooting under strategy (i), eqn. [7.6], where a proportion of the excess of females over a threshold are shot.

Consider first the deterministic model with constant recruitment, $\bar{b}$, and survival, $\bar{S}$. Substituting [7.6] for H_t in [7.5] yields

$$N_{t+1} = \bar{b}\left(N_t - ca\left[N_t - T\right]_+\right) + \bar{S}\left(N_t - a\left[N_t - T\right]_+\right) \qquad [A2.1]$$

where the shorthand notation $[\ ]_+$ is defined by the rule $[x]_+ = x$ if $x > 0$ and zero otherwise.

The map of N_{t+1} against N_t is illustrated in Fig. A2.1 with the deterministic equilibrium $\bar{N}$ given by

$$\bar{N} = \frac{aT\left(c\bar{b} + \bar{S}\right)}{1 - \bar{b} - \bar{S} + a\left(c\bar{b} + \bar{S}\right)} \qquad [A2.2]$$

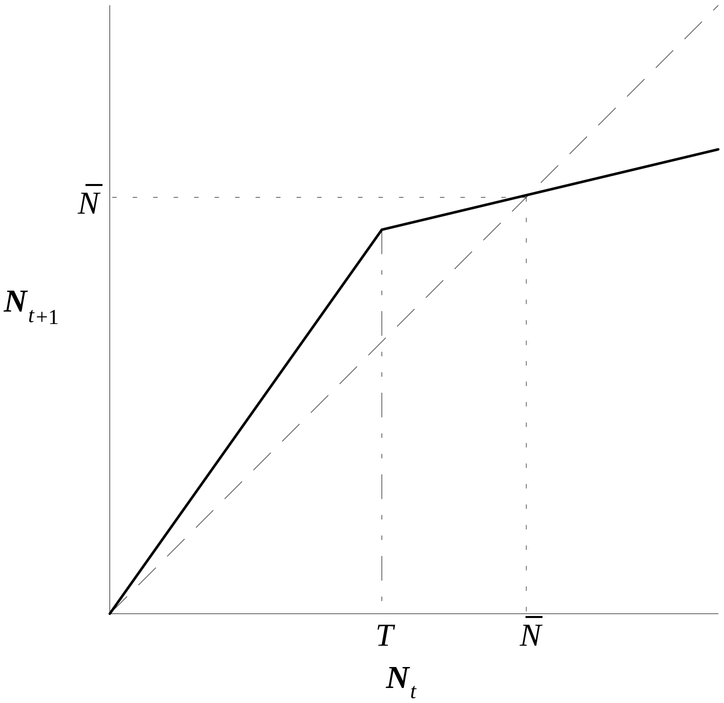


Figure A2.1. Map of N_{t+1} against N_t for the goose model with shooting a constant fraction of the females above a threshold [A2.1].

The model is linear in the region of the equilibrium: this is obvious if [A2.1] is written in the form

$$N_{t+1} = \left[\bar{b}(1-ca) + \bar{S}(1-a)\right]N_t + aT\left(c\bar{b} + \bar{S}\right) \qquad \left(N_t > T\right) \tag{A2.3}$$

To investigate the effect of fluctuating vital rates n_t, $v_{b,t}$ and $v_{S,t}$ are introduced as deviations from the mean values of number of female geese, recruitment and survival respectively such that

$$\begin{aligned} N_t &= \bar{N} + n_t \\ S_t &= \bar{S} + v_{S,t} \\ b_t &= \bar{b} + v_{b,t} \end{aligned} \tag{A2.4}$$

Inserting [A2.4] in [A2.3], expanding, and discarding terms which involve products of any two of n_t, $v_{b,t}$ or $v_{S,t}$ yields an approximation for the deviation from the mean population size

$$n_{t+1} = \alpha n_t + Z_t \tag{A2.5}$$

where

$$\begin{aligned} \alpha &= \bar{b}(1-ca) + \bar{S}(1-a) \\ Z_t &= \frac{aT\left[v_{b,t}\left(c - c\bar{S} + \bar{S}\right) + v_{S,t}\left(1 - \bar{b} + c\bar{b}\right)\right]}{1 - \bar{b} - \bar{S} + a\left(c\bar{b} + \bar{S}\right)} \end{aligned} \tag{A2.6}$$

The approximation [A2.5] is a first order autoregressive process with variance given by (Chatfield 1984)

$$\sigma_n^2 = \frac{\sigma_Z^2}{1-\alpha^2} \tag{A2.7}$$

Note that a similar approximation process for the model with shooting defined by eqn. [7.7], where the number shot is based on the number of females on Islay in the previous winter, would produce a second order autoregressive process. For independent recruitment and survival, with variances σ_b^2 and σ_S^2 respectively, the variance of Z_t is given by

$$\sigma_Z^2 = \frac{a^2T^2\left[\sigma_b^2\left(c - c\bar{S} + \bar{S}\right)^2 + \sigma_S^2\left(1 - \bar{b} + c\bar{b}\right)^2\right]}{\left[1 - \bar{b} - \bar{S} + a\left(c\bar{b} + \bar{S}\right)\right]^2} \tag{A2.8}$$

Fig. A2.2 compares the variance in n_t obtained from simulations of [A2.1] with that given by the approximation [A2.7]. As the variance of Z_t increases, the approximation [A2.7] tends to underestimate the actual variance in the deviation

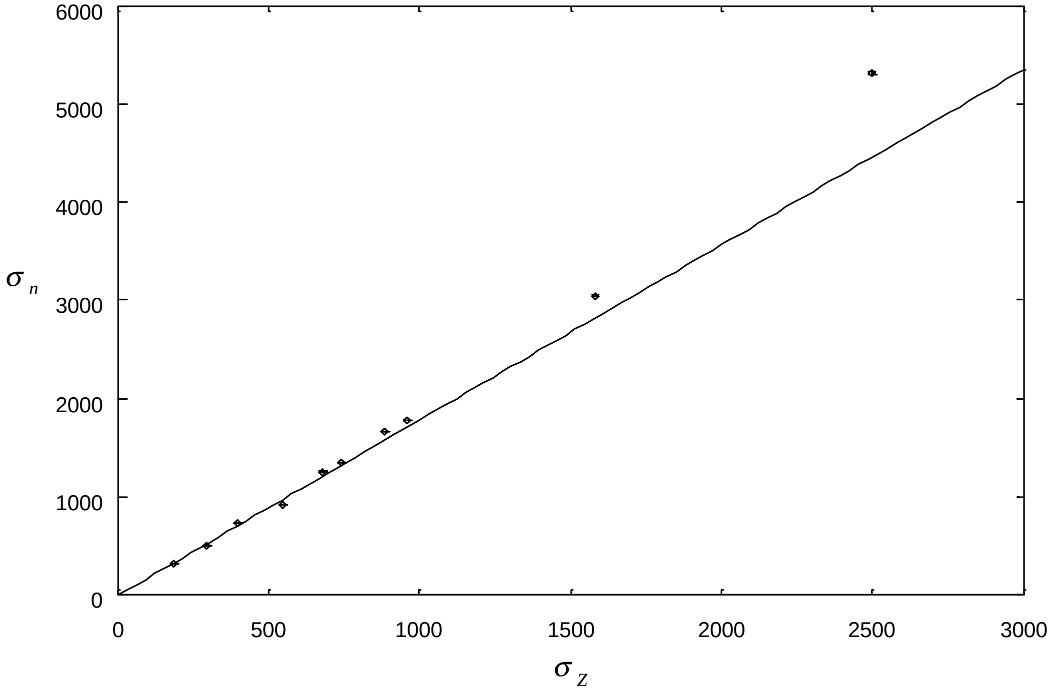


Figure A2.2. Standard deviation of the departure from equilibrium population size, σ_n, as the environmental standard deviation, σ_Z, increases. Line: approximation of eqn. [A2.7]; points: mean standard deviation (with 95% confidence interval) for 5000 simulations, each of 1000 years, of the full model [A2.1].

from the deterministic equilibrium population size. The point with the highest variances in Fig. A2.2 corresponds to the values calculated for the Islay wintering barnacle geese from the data of Table 7.1 (chapter 7).

In addition to underestimating the variance in population size at higher levels of the input variance, the first order autoregressive approximation also overestimates the mean population size. While the approximation [A2.5] suggests the average deviation from the deterministic equilibrium [A2.2] will be zero, the simulations carried out confirm that, in common with Roughgarden's (1975) stochastic logistic, the mean population size when the vital rates are varying is generally less than the deterministic equilibrium. For the variance in recruitment and survival measured from the Islay goose data of Table 7.1 the mean deviation, $\bar{n}$, from the deterministic equilibrium is -1272.7 (measured over 5000 replicates of 1000 years).

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