Stochastic modelling of environmental variation for biological populations

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Abstract

We examine stochastic effects, in particular environmental variability, in population models of biological systems. Some simple models of environmental stochasticity are suggested, and we demonstrate a number of analytic approximations and simulation-based approaches that can usefully be applied to them. Initially, these techniques, including moment-closure approximations and local linearization, are explored in the context of a simple and relatively tractable process. Our presentation seeks to introduce these techniques to a broad-based audience of applied modellers. Therefore, as a test case, we study a natural stochastic formulation of a non-linear deterministic model for nematode infections in ruminants, proposed by Roberts and Grenfell (1991). This system is particularly suitable for our purposes, since it captures the essence of more complicated formulations of parasite demography and herd immunity found in the literature.

We explore two modes of behaviour. In the *endemic regime* the stochastic dynamic fluctuates widely around the non-zero fixed points of the deterministic model. Enhancement of these fluctuations in the presence of environmental stochasticity can lead to extinction events. Using a simple model of environmental fluctuations we show that the magnitude of this system response reflects not only the variance of environmental noise, but also its autocorrelation structure. In the *managed regime* host-replacement is modelled via periodic perturbation of the population variables. In the absence of environmental variation stochastic effects are negligible, and we examine the system response to a realistic environmental perturbation based on the effect of micro-climatic fluctuations on the contact rate. The resultant stochastic effects, and the relevance of analytic approximations based on simple models of environmental stochasticity, are discussed.

1   Introduction

The inclusion of stochasticity in a mathematical model may be motivated by several factors. For example, Rand and Wilson (1991) partition stochastic effects for epidemics into three types: i) demographic fluctuations arising from the stochastic nature of the epidemic; ii) randomness in the environment, and thereby in the parameters affecting the epidemic; and, iii) measurement errors. The first two have the potential to make stochastic model behaviour quite distinct from that of a deterministic implementation (see, for example, Gurney and Middleton, 1996; Wilson and Hassell, 1997; Kokko and Ebenhard, 1996; Marion *et al.*, 1998), and these effects should be considered in any modelling study.

Marion *et al.* (1998) consider type (i) stochasticity in a reformulation of a deterministic model of nematode infection of ruminants proposed by Roberts and Grenfell (1991). Such demographic stochasticity is shown to be important in terms of extinction events and equilibrium model behaviour (the *endemic regime*), but muted in a transitory *managed regime* where the system is periodically perturbed. In the absence of an explicit solution, various analytic approximations are evaluated in the light of simulations of the stochastic model. Here we extend the scope of this earlier paper to include deterministic and stochastic fluctuations in the model parameters. Environmental fluctuations are seen as crucial in modelling commercially important nematode infections (see, for example, Beecham, 1997; Barnes *et al.*, 1988; Callinan *et al.*, 1982; Grenfell *et al.*, 1987; Thomas *et al.*, 1986), and many other biological systems. For example, Jhost and Wissel (1997) study the influence of temporal correlations in stochastic environmental fluctuations on extinction risk, and Gurney and Middleton (1996) show that random variations in the environment crucially alter optimal resource allocation strategies. Roberts and Grenfell (1992) examine deterministic environmental fluctuations in their deterministic model of nematode infection (Roberts and Grenfell, 1991), and this deterministic variation can be handled in a stochastic model using the methods presented in Marion *et al.* (1998). We shall therefore focus on the development of techniques such as local linearization, moment-closure approximations and simulation, as applied to stochastic environmental fluctuations.

Our principal aims are to present a generally applicable framework which accounts for both demographic and environmental stochasticity in population biology, and to show how to conduct simulations and derive analytic approximations for such models. We also seek to promote wider use of stochastic methods. Stochastic analogues of many deterministic models are readily identified and simulation is usually straight-forward (see Section 2.1). Analytic approximations are a useful way of exploring model behaviour, and often provide valuable insight. We compare two such approximation schemes. The first, moment closure, has no direct analogue in deterministic modelling, but may be interpreted in terms of distributional assumptions akin to the negative binomial distribution of host parasite burden assumed by Anderson and May (1978). The second is based on local linearization of a stochastic differential formulation of the model, and is an extension of the transfer function approach used by Roberts and Grenfell (1992) to analyze environmental perturbations in a deterministic model (see also Nisbet and Gurney, 1982).

To illustrate these ideas we first consider the immigration-death model (Section 2), where simple models of environmental variation are introduced, and incorporated into moment-closure and local linear approximations. These procedures are compared with simulations, and, where possible, with

exact results. In Section 3 we describe our model of helminth infection, and show how to derive approximations under different parameter perturbations. In Section 4 approximations are compared with simulations in the endemic regime. In particular, we study deterministic fluctuations, and the effect of temporal correlations in stochastic parameter variation on extinction risk. Finally, Section 5 uses the methods to explore the effects of fluctuations in the contact rate of the infection which results from a mechanistic model of helminth response to micro-climatic fluctuations developed by Beecham (1997). This analysis is conducted in a managed regime where stochastic effects are negligible in the absence of environmental perturbation.

2 Environmental variation and a solvable model

2.1 Formulation and analysis of stochastic models

The immigration-death model consists of a single population of size $n(t)$ which changes in a small time interval $(t, t + \Delta t)$ according to the probabilities

$$\Pr(n(t + \Delta t) = n(t) + 1) = \nu(t)\Delta t \,, \qquad \Pr(n(t + \Delta t) = n(t) - 1) = \mu(t)n(t)\Delta t \,. \qquad (2.1)$$

In general, the *death rate* $\mu(t)$ and *immigration rate* $\nu(t)$ are time-dependent. Statement of these birth-death probabilities specifies the stochastic model, just as specification of the rates $\nu(t)$ and $\mu(t)x(t)$ defines the deterministic model $dx(t)/dt = \nu(t) - \mu(t)x(t)$. This correspondence is readily extended to more complex models, and the continuous-valued population level $x(t)$ of the deterministic model coincides with the true expected population size $\mathbf{E}[n(t)]$ when the transition probabilities are linear functions of the stochastic variables. We shall consider three cases in which ν and μ are constant, vary deterministically, and vary stochastically.

(i) Constant environment: For time-independent transition rates, simulation of the stochastic model is straightforward since the inter-event time is exponentially distributed with rate $R = \nu + \mu x$ (see Renshaw, 1991). *Chapman-Kolmogorov forward equations* typically form the basis for analysis of stochastic population models (see, for example, Cox and Miller, 1965), and are formed by considering all possible events occurring in a short time interval $(t, t + \Delta t)$. Multiple events occur with negligible probability and can be ignored. Let $p(n; t)$ denote the probability of obtaining a population of size n at time t given a population of size n_0 at $t = 0$. Then the forward equation is

$$dp(n; t)/dt = p(n - 1; t)\nu + p(n + 1; t)(n + 1)\mu - p(n; t)(\nu + \mu n) \,. \qquad (2.2)$$

Introduction of the *moment generating function* (m.g.f.) $M(\theta; t) \equiv \mathbf{E}\left[e^{\theta n}\right] \equiv \sum_{n=0}^{\infty} e^{\theta n} p(n; t)$ enables raw moments of the process (i.e. $\mathbf{E}\left[n^j\right] : j = 1, 2, ...$) to be derived by evaluating $\partial^j M(\theta; t)/\partial \theta^j$ at $\theta = 0$. This can be seen by expanding $\mathbf{E}\left[e^{\theta n}\right] = \mathbf{E}\left[1 + \theta n + \theta^2 n^2/2! + ...\right]$.

Multiplying (2.2) by $\exp\{\theta n\}$ and summing over $n = 0, 1, 2, ...$ results in the equation

$$\partial M/\partial t = \nu(e^\theta - 1)M + \mu(e^{-\theta} - 1)\partial M/\partial \theta \,. \qquad (2.3)$$

Since ν and μ are constant, it is straightforward to solve this for the *cumulant generating function* (c.g.f.), $K(\theta; t) \equiv \ln M(\theta; t)$, using the method of auxiliary equations (Bailey, 1964; Cox and Miller, 1965) obtaining

$$K(\theta; t) \equiv \sum_{j=1}^{\infty} \theta^j \kappa_j(t)/j! = n_0 \ln\{1 - e^{-\mu t}(1 - e^\theta)\} - (1 - e^{-\mu t})(1 - e^\theta)(\nu/\mu) \,, \qquad (2.4)$$

where $\kappa_j(t)$ is the cumulant of order j at time t. For example, κ_1 is the mean $\mathbf{E}[x]$, and κ_2 the variance $\mathbf{E}[x^2] - \mathbf{E}[x]^2$, whilst the third- and fourth-order cumulants measure skewness and kurtosis (Kendall, 1994). Note that if $n_0 = 0$, then all the cumulants are equal, since $\kappa_j(t) \equiv (1 - e^{-\mu t})(\nu/\mu)$, which is a characteristic of the Poisson distribution.

(ii) Deterministic variation: For time-varying parameters $\nu(t)$ and $\mu(t)$, given an event at t_0, the time of the next event t_1 is obtained by first drawing τ from an exponential distribution with unit mean, and then solving

$$\tau = \int_{t_0}^{t_1} [n(t_0)\mu(t) + \nu(t)]dt \qquad (2.5)$$

for t_1. Alternatively, an approximate simulation method is to increment time by an appropriately small step Δt, and use the probabilities (2.1) to determine which event, if any, occurs in $(t, t + \Delta t)$.

When $\nu(t)$ and $\mu(t)$ vary deterministically the forward equation is identical to (2.3), but with ν and μ replaced by $\nu(t)$ and $\mu(t)$, namely

$$\partial K/\partial t \;=\; \nu(t)(e^\theta - 1) + \mu(t)(e^{-\theta} - 1)\partial K/\partial\theta. \qquad (2.6)$$

Appendix A describes how to solve this equation in general, and a closed form solution is obtained for the case of constant death rate and sinusoidally varying immigration rate $\nu(t) = \nu_0[1 + \epsilon\cos(\omega t + \phi)]$. In this case we obtain expressions for the cumulants, and show that the population fluctuations follow a Poisson distribution when the initial population is zero ($n_0 = 0$).

When both transition rates are time-dependent we are unable to find a closed form solution, and such intractability is common to many realistic models of biological systems. Nevertheless, some progress can be made. Expression (2.4) shows that the c.g.f. may be expanded in terms of the cumulants κ_j, whence differentiating (2.6) with respect to θ (at $\theta = 0$) leads to a closed set of ordinary differential equations for the κ_j up to any desired order. For example, the mean $\kappa_1 = \mathbf{E}[n]$ and variance $\kappa_2 = \mathbf{E}[n^2] - \kappa_1^2$ are given by

$$
\begin{aligned}
d\kappa_1/dt &= \nu(t) - \mu(t)\kappa_1 \qquad (2.7)\\
d\kappa_2/dt &= \nu(t) + \mu(t)(\kappa_1 - 2\kappa_2).
\end{aligned}
$$

If necessary, generalizations of (2.7) may be integrated numerically. An approximation to the distribution $p(n; t)$ may be obtained from a finite number of cumulants. For example, κ_1 and κ_2 may parameterize the Normal or, depending on the ratio of the mean to variance, the binomial, Poisson or negative binomial distributions (see Renshaw, 1991). For $\mu(t) = 1$ and $\nu(t) = 1 + \cos(t)$, Figure 1a compares the exact probability $p(0; t)$ (see Appendix A) with its highly accurate binomial approximation (so here $\kappa_2 < \kappa_1$), and to the Normal approximation which is clearly too large for small t and too low for $t > 2$. Figure 1b shows that the binomial approximation to κ_3 is also accurate, whilst the Normal approximation, for which $\kappa_3 = 0$, fairs poorly in comparison. Note that when $n_0 = 0$ the true distribution is Poisson.

(iii) Continuous stochastic variation: One approach is to model the parameters themselves using discrete stochastic processes. This results in a higher-dimensional model which may be non-linear in the stochastic variables, such as the term $n(t)\mu(t)$ for stochastically varying death rate in

the immigration-death model. Nevertheless, several authors have considered discrete-valued multi-dimensional non-linear stochastic processes (see Isham, 1991; Marion *et al.*, 1998), and we shall not explore this approach further here. Instead, we focus on continuous stochastic variation.

In Appendix B we adopt a continuous limit of a discrete random walk, namely the mean-reverting Uhlenbeck-Ornstein process, as our model of continuous stochastic environmental noise, taking model parameters as transformations of this process. For example, in the immigration-death model $\nu = B(Z_\nu)$, the mean-reverting Uhlenbeck-Ornstein processes, Z_ν, has a Normal distribution and with (in equilibrium) mean $\bar{Z}_\nu$ and variance $\sigma_\nu^2/2b_\nu$ (see text following Eq. B.7). In Section 2.2 the parameter b_ν is seen to control the auto-correlation of Z_ν.

Two possible transformations are $\nu = B(Z_\nu) = Z_\nu^2$, which imposes a Normal distribution on $\sqrt{\nu}$, and the log-Normal transformation $\nu = B(Z_\nu) = \exp\{Z_\nu\}$. In each case we parameterize the underlying process (for a given b_ν) by matching the required mean $\mathbf{E}[\nu]$ and variance $\mathrm{var}[\nu]$ with those of $B(Z_\nu)$. When $B(Z_\nu) = \exp\{Z_\nu\}$ this yields

$$
\begin{aligned}
\bar{Z}_\nu &= 2\ln\{\mathbf{E}[\nu]\} - \ln\{\mathrm{var}[\nu] + \mathbf{E}[\nu]^2\}/2 \\
\sigma_\nu^2 &\equiv 2b_\nu\sigma_{Z_\nu}^2 = 2b_\nu[\ln\{\mathrm{var}[\nu] + \mathbf{E}[\nu]^2\} - 2\ln\{\mathbf{E}[\nu]\}];
\end{aligned}
\tag{2.8}
$$

whilst for the case $B(Z_\nu) = Z_\nu^2$,

$$
\bar{Z}_\nu^2 = \left(\mathbf{E}[\nu]^2 - \mathrm{var}[\nu]/2\right)^{1/2} \quad \text{and} \quad \sigma_\nu^2 \equiv 2b_\nu\sigma_{Z_\nu}^2 = 2b_\nu\left[\mathbf{E}[\nu] - \bar{Z}_\nu^2\right],
\tag{2.9}
$$

where we have defined $\sigma_{Z_\nu}^2$ for later convenience. Note that the latter expression for $\bar{Z}_\nu$ places a restriction between the mean and variance of ν ($\mathrm{var}[\nu] \leq 2\,\mathbf{E}[\nu]^2$). In Section 2.2 we consider the effect of b_ν on population fluctuations, but until then we assign $b_\nu = 0.5$ (that is, $\sigma_\nu = \sigma_{Z_\nu}$).

Moment closure and the Normal approximation: Appendix B shows how to construct the associated Chapman-Kolmogorov forward equation (B.4) for the joint-density of the population and environmental fluctuations for the immigration-death model together with the corresponding m.g.f. equation (B.5). Consider constant death rate $\mu(t) = \mu_0$, and variation in the immigration rate modelled as a transformation of a mean-reverting Uhlenbeck-Ornstein process $\nu = B(Z_\nu)$. The appropriate substitutions, $\alpha_\mu = \beta_\mu = 0$, $D(Z_\nu) = \mu_0$, $\alpha_\nu = \sigma_\nu^2$ and $\beta_\nu = b_\nu(\bar{Z}_\nu - Z_\nu)$ reduce Eq. (B.5) to

$$
\frac{\partial M}{\partial t} = (e^{n\theta} - 1)\hat{B}(\partial/\partial\lambda_\nu)M + (e^{-n\theta} - 1)\mu\partial M/\partial\theta + \lambda_\nu^2\sigma_\nu^2 M/2 + \lambda_\nu b_\nu\left(\partial M/\partial\lambda_\nu + \bar{Z}_\nu\right).
\tag{2.10}
$$

The case $\nu = B(Z_\nu) = Z_\nu$ is analytically tractable, but allows the immigration rate to be negative (it is Normally distributed) and so will not be considered further. In general, no analytic solutions have been obtained, but taking appropriate first- and second-order derivatives of Eq. (2.10) with respect to θ and λ_ν, and setting $\theta = \lambda_\nu = 0$, leads to

$$
\begin{aligned}
d\mathbf{E}[n]/dt &= \mathbf{E}[B(Z_\nu)] - \mu_0\mathbf{E}[n] \\
d\mathbf{E}[n^2]/dt &= \mathbf{E}[B(Z_\nu)] + 2\mathbf{E}[nB(Z_\nu)] + \mu_0\mathbf{E}[n] - 2\mu_0\mathbf{E}[n^2] \\
d\mathbf{E}[nZ_\nu]/dt &= \mathbf{E}[Z_\nu B(Z_\nu)] - \mu_0\mathbf{E}[nZ_\nu] + b_\nu Z_\nu\mathbf{E}[n] - b_\nu\mathbf{E}[nB(Z_\nu)],
\end{aligned}
\tag{2.11}
$$

together with equations for the first two moments of $Z_\nu(t)$ which satisfy (B.7). Equations for higher-order moments can be obtained in a similar fashion. Note that this is analogous to the derivation of the cumulant equations (2.7).

If $B(Z_\nu)$ is non-linear then the equation for any given moment involves moments of higher-order, and so the system (2.11) cannot be closed; a parallel problem arises in the corresponding cumulant equations. However, closure may be imposed by assuming that cumulants above a certain order are zero (see, for example, Matis *et al.*, 1998). Second-order cumulant truncation, where only the mean and variance-covariances are assumed non-zero, relates to a Gaussian distribution. As an example of this *Normal approximation*, consider the case $\nu = B(Z_\nu) = Z_\nu^2$. Recall that in one dimension the c.g.f. can be expanded as $K(\theta) = \theta\kappa_1 + \theta^2\kappa_2/2! + \theta^3\kappa_3/3! + O(\theta^4)$. In this case, second-order cumulant truncation yields $K_2(\theta) = \theta\kappa_1 + \theta^2\kappa_2/2!$ which corresponds to a Normal distribution. Approximate higher-order moments can be obtained, via the m.g.f. $M_2(\theta) = \exp\{K_2(\theta)\} \approx \mathbf{E}[\exp\{n\theta\}]$. A two-dimensional analogue of this argument yields

$$M_2(\theta, \lambda_{z_\nu}) \equiv \exp\{K_2(\theta, \lambda_{z_\nu})\} \tag{2.12}$$
$$K_2(\theta, \lambda_{z_\nu}) \equiv \kappa_{10}\theta + \kappa_{01}\lambda_{z_\nu} + \kappa_{20}\theta^2/2 + \kappa_{11}\theta\lambda_{z_\nu} + \kappa_{02}\lambda_{z_\nu}^2/2\,.$$

For the immigration-death model, when $\nu = B(Z_\nu) = Z_\nu^2$, we have $\kappa_{10} = \mathbf{E}[n]$, $\kappa_{01} = \mathbf{E}[Z_\nu]$, κ_{20} and κ_{02} correspond to the variances of n and Z_ν, respectively, whilst κ_{11} is their covariance. Closure of the moment update equations (2.11) can now be achieved by noting that for the truncated process

$$\mathbf{E}[Z_\nu^3] = \partial^3 M_2(\theta, \lambda_{z_\nu})/\partial\lambda_{z_\nu}^3\,|_{\theta=\lambda_{z_\nu}=0} \quad \text{and} \quad \mathbf{E}[nZ_\nu^2] = \partial^3 M_2(\theta, \lambda_{z_\nu})/\partial\theta\partial\lambda_{z_\nu}^2\,|_{\theta=\lambda_{z_\nu}=0}\,. \tag{2.13}$$

The next order of approximation requires derivation of the moment evolution equations to third-order. However, recent work based on univariate saddlepoint approximations suggests that increased accuracy need not necessarily follow from higher-order cumulant truncation (Renshaw, 1998).

It should be noted that this problem of closure is widespread in population biology since it relates to any nonlinear stochastic model. In the remainder of this paper we apply the Normal approximation (second-order cumulant truncation) which was originally proposed by Whittle (1957) and used subsequently by Isham (1991), who applies it to epidemic models, and Grenfell *et al.* (1995a,b) who study macro-parasitic infections.

Simulations: Since we have not yet obtained full analytic solutions, the Normal approximation is compared with stochastic simulation. For simplicity, we ignore the transient system response and focus on equilibrium behaviour. Perturbation of the immigration rate means that the inter-event time (2.5) is now determined by a stochastic integral, so we approximate the dynamics by incrementing time by a small step Δt, and updating the population variable n according to the probabilities (2.1). To simulate the continuous-valued environmental noise process, one approach is to update $\nu(t) = Z_\nu(t)^2$ according to the stochastic difference equation

$$Z_\nu(t + \Delta t) = Z_\nu(t) + b_\nu[\bar{Z}_\nu - Z_\nu]\Delta t + \sigma_\nu\eta(t)\sqrt{\Delta t}\,, \tag{2.14}$$

where $\eta(t)$ is a white noise process of zero mean and unit variance (Nisbet and Gurney, 1982). Comparison with the text following Eq. (B.6) shows that the mean and variance of these updates are equivalent to the instantaneous mean, $\beta_\nu = b_\nu[\bar{Z}_\nu - Z_\nu]$, and variance, $\alpha_\nu = \sigma_\nu^2$, of the corresponding mean-reverting Uhlenbeck-Ornstein velocity process.

Table I shows the mean and variance of the population fluctuations based on 1000 simulations of the immigration-death model over $t = 0, ..., 1000$, with the parameter values shown. Equilibrium

values obtained from the Normal approximation are also presented. The results demonstrate that as the variance of the environmental noise increases; fluctuations in the population increase; the Normal approximation increasingly under-estimates the population variances, and the true distribution becomes increasingly skewed. This breakdown of the Normal approximation, which allows negative population sizes, is illustrated in Figure 2 which shows the corresponding Normal distribution alongside histograms of samples taken from these simulations following a burn-in period.

2.2 An alternative approach

We now examine the relevance of stochastic differential equations (s.d.e's) to the treatment of parameter variation and uncertainty. In the immigration-death model, the update, $n(t + \Delta t) - n(t)$ is governed by the birth-death probabilities (2.1), and to order $O(\Delta t^2)$ has mean and variance

$$
\begin{aligned}
f(n, \mathbf{u}(t))\Delta t &\equiv (+1)P(n(t + \Delta t) = n(t) + 1) + (-1)P(n(t + \Delta t) = n(t) - 1)) \\
&= [\nu(t) - \mu(t)n(t)]\Delta t, \hspace{3cm} (2.15) \\
q(n, \mathbf{u}(t))\Delta t &\equiv (+1)^2 P(n(t + \Delta t) = n(t) + 1)) + (-1)^2 P(n(t + \Delta t) = n(t) - 1)) \\
&= [\nu(t) + \mu(t)n(t)]\Delta t,
\end{aligned}
$$

respectively. Here $\mathbf{u}(t)^T = (\nu(t), \mu(t))$. Now consider a continuous-valued, stochastic variable $x(t)$ representing the population size in the s.d.e. formulation. In a small interval $(t, t + \Delta t)$ the change in $x(t)$ is

$$
\Delta x(t) = x(t + \Delta t) - x(t) = f(x, \mathbf{u}(t))\Delta t + q^{1/2}(x, \mathbf{u}(t))\Delta t^{1/2}\eta(t), \hspace{2cm} (2.16)
$$

where $\eta(t)$ is a white noise process of zero mean and unit variance. The expectation and variance of the update $\Delta x(t)$ therefore correspond to those of (2.15) for the discrete-valued process $n(t)$. On dividing (2.16) through by Δt, and letting $\Delta t \to 0$, we obtain

$$
dx(t)/dt = f(n, \mathbf{u}(t)) + q(x, \mathbf{u}(t))^{1/2}\gamma(t), \hspace{3cm} (2.17)
$$

where $\gamma(t) = \lim_{\Delta t \to 0} \eta(t)/\Delta t^{1/2}$ is the time derivative of a Weiner process of zero mean and unit variance; for a rigorous treatment of s.d.e's see Mao (1997). The first term on the right hand side of (2.17) corresponds to the deterministic model, whilst the second accounts for demographic fluctuations inherent in the probabilities (2.1). Note that the continuous-valued $x(t)$ can be regarded as an approximation to the discrete-valued process $n(t)$.

In Appendix C we formulate a more general stochastic differential equation model with k interacting populations $\mathbf{n}^T = (n_1, n_2, ..., n_k)$, and time varying parameters $\mathbf{u}(t)^T = (u_1(t), u_2(t), ..., u_p(t))$ (see Eq. C.3). Both deterministic and continuous stochastic parameter fluctuations are considered. At present no general solution exists for such stochastic differential equations (see Mao, 1997). Nevertheless progress can be made by linearization. We assume that the variation of parameters about some constant level is small, i.e. $\mathbf{u}(t) = \mathbf{u}_0 + \delta\mathbf{u}(t)$, and that these fluctuations may be decomposed into a sum of a sinusoidal deterministic component $\delta\mathbf{d}(t)$ and a zero mean stochastic element $\delta\mathbf{r}(t)$. If the deterministic equation $d\mathbf{x}/dt = f(\mathbf{x}, \mathbf{u}_0)$ has a fixed point $\mathbf{x}_1$, the corresponding s.d.e. can then be linearized. The linearized equations, which are strictly valid for large times only, are then solved and we present expressions for the expectations $\mathbf{E}[x_l]$ and the time-lagged

cross- and auto-correlations $\mathcal{C}_{x_l x_m}(\tau)$ of the equilibrium population fluctuations (see Eqs. C.11 and C.14). $\mathcal{C}_{x_l x_m}(\tau)$ measures the degree of correlation between fluctuations in population l at time t and population m at time $t + \tau$. Note that the population variances and covariances are given by $\mathcal{C}_{x_l x_m}(\tau = 0)$. Equation (C.14) shows that these fluctuations can be decomposed into a sum of terms attributable to deterministic parameter fluctuations, and to demographic and environmental stochasticity, respectively. Our aim is that Appendix C be regarded as a template for a wide range of population models, and its use is now illustrated by application to the immigration-death model.

Application to immigration-death model: We now compare the results derived from a linearized s.d.e. formulation of the immigration-death model with Normal approximations and, where available, with exact results. Note that the results of Appendix C apply asymptotically, and so we must compare them with those derived in Section 2.1 in the limit as $t \to \infty$.

(i) Demographic stochasticity: In terms of the general form (C.3) the immigration-death model is one-dimensional ($k = 1$) with $\mathbf{u}^T = (\nu(t), \mu(t))$, and f_1 and q_1 defined in Eq. (2.15). Let the death rate $\mu = \mu_0$ be constant, and the immigration rate fluctuate about ν_0. Linearization is performed around $\mathbf{u}_0^T = (\nu_0, \mu_0)$ and $\mathbf{x}_1 = \nu_0/\mu_0$ (i.e. $f_1(\mathbf{x}_1, \mathbf{u}_0) = 0$), so $q_1(x_1, \nu_0, \mu_0) = 2\nu_0$. Then the transfer function (see Eq. C.7) is $T(\omega) = [i\omega + \mu_0]^{-1}$, and the demographic fluctuation (C.17) is given by

$$
\begin{aligned}
\mathcal{C}_{x\,x}^{\text{dem}}(\tau) &= \frac{1}{2\pi} \int_{-\infty}^{+\infty} q_1(x_1, \nu_0, \mu_0) \, |T(\omega)|^2 \exp(i\omega\tau) d\omega \\
&= \frac{\nu_0}{\pi} \int_{-\infty}^{+\infty} [\exp(i\omega\tau)/(\omega^2 + \mu_0^2)] d\omega = \nu_0 \exp(-\mu_0 \tau)/\mu_0 \, .
\end{aligned}
\tag{2.18}
$$

See, Gradshteyn and Ryzhik (1965, p. 217) for evaluation of this integral. Note that the generating function approach is not used to calculate time-lagged correlations, only moments and cumulants of the population distribution at time t. Here we are interested in $\mathcal{C}_{xx}^{\text{dem}}(\tau = 0) = \nu_0/\mu_0$ which, for $t \to \infty$, corresponds to the population variance in the absence of any environmental perturbation (see text following Eq. 2.4).

Another example of solely demographic stochasticity is provided by the mean-reverting Uhlenbeck-Ornstein process itself. Comparison of expressions (C.2) and (2.14) reveals that, in this case $k = 1$, $f_1 = b_\nu[\bar{Z}_\nu - Z_\nu]$ and $q_1 = \sigma_\nu^2$. Note also that the parameters $\mathbf{u}^T = (b_\nu, \sigma_\nu, \bar{Z}_\nu)$ are constant. It follows that $T(\omega) = [i\omega + b_\nu]^{-1}$ and $\bar{Z}_\nu$ is the fixed point of the deterministic dynamics. Therefore, from (C.17) the equilibrium autocorrelation of the process is

$$
\mathcal{C}_{Z_\nu Z_\nu}^{\text{dem}}(\tau) = \frac{\sigma_\nu^2}{2\pi} \int_{-\infty}^{+\infty} \exp(i\omega\tau)/(\omega^2 + b_\nu^2) d\omega = \sigma_\nu^2 \exp(-b_\nu \tau)/2b_\nu \, .
\tag{2.19}
$$

Thus, Z_ν has exponentially decaying autocorrelation, with parameter b_ν controlling the rate of decay. Furthermore, this expression reveals that for the mean-reverting Uhlenbeck-Ornstein process, the spectral density $\mathcal{S}_{Z_\nu Z_\nu}(\omega) = \sigma_\nu^2/(\omega^2 + b_\nu^2)$, since by definition its inverse Fourier transform is the autocorrelation, i.e. $\mathcal{C}_{Z_\nu, Z_\nu}(\tau) = \int_{-\infty}^{\infty} \mathcal{S}_{Z_\nu, Z_\nu}(\omega) \exp(i\omega t) d\omega/2\pi$.

(ii) Deterministic variation: Consider constant death rate $\mu = \mu_0$, and let the immigration rate vary sinusoidally as $\nu = \nu_0 + \epsilon\nu_0 \cos(\omega t)$. Then Eq. (C.12) defines the phase shift $\xi(\omega) = \tan^{-1}(-\omega/\mu_0)$, and on using Eq. (C.11) the expected displacement is approximated by

$$
\mathbf{E}\,[x(t)] = (\nu_0/\mu_0) + \epsilon\nu_0 \cos(\omega t - \tan^{-1}(\omega/\mu_0))/\sqrt{\mu_0^2 + \omega^2} \, ,
\tag{2.20}
$$

which agrees with the exact result derived from Eq. (A.2).

(iii) Response to temporal correlations in environmental fluctuations: Assume a constant death rate as above, but now let the immigration rate be described by a transformed mean-reverting Uhlenbeck-Ornstein process, $\nu = B(Z_\nu)$. Adapting the calculation (2.18) above, it is straightforward to show that the demographic term is now $\mathcal{C}_{x\,x}^{\text{dem}}(\tau) = B(\bar{Z}_\nu)\exp(-\mu_0\tau)/\mu_0$. Similarly, using Eq. (C.16) the variance of population fluctuations induced by this environmental noise is

$$\mathcal{C}_{x\,x}^{\text{ran}}(\tau=0) \;=\; \frac{1}{2\pi}\int_{-\infty}^{+\infty}|T(\omega)|^2\,(\partial f/\partial Z_\nu)^2\mathcal{S}_{Z_\nu Z_\nu}(\omega)d\omega\,. \tag{2.21}$$

If $\nu(t) = B(Z_\nu)$ is Z_ν^2 or $\exp(Z_\nu)$, and the parameters of the noise model are obtained from expressions (2.9) and (2.8), respectively, we find that $\sigma_\nu^2 = 2b_\nu\sigma_{Z_\nu}^2$. The dependence of the spectral density on b_ν, namely $\mathcal{S}_{Z_\nu Z_\nu}(\omega) = 2b_\nu\sigma_{Z_\nu}^2/(\omega^2+b_\nu^2)$, is obtained on using the definition of $\mathcal{S}_{Z_\nu Z_\nu}(\omega)$ following Eq. (2.19), whence

$$\mathcal{C}_{x\,x}^{\text{ran}}(\tau=0) \;=\; \left(\partial B(\bar{Z}_\nu)/\partial Z_\nu\right)^2\sigma_{Z_\nu}^2/\left[\mu_0(b_\nu+\mu_0)\right] \tag{2.22}$$

which is maximized for $b_\nu \to 0$. This response to the colour of the environmental noise can also be understood in terms of the frequency response of the system to sinusoidal perturbations. Equation (C.11) shows that the magnitude of a sinusoidal perturbation in Z_ν is scaled by the factor $|T(\omega)|\,\partial f(\mathbf{x}_1,\bar{Z}_\nu,\mu_0)/\partial Z_\nu$ which, in the present case, is maximized by $\omega^* = 0$. Now, for $|T(\omega)|$ sufficiently peaked around ω^*, the population variance (2.21) can be further approximated as

$$\mathcal{C}_{x\,x}^{\text{ran}}(\tau=0) \approx \frac{1}{2\pi}|T(\omega^*)|^2\,(\partial f/\partial Z_\nu)^2\mathcal{S}_{Z_\nu Z_\nu}(\omega^*) \tag{2.23}$$

which is largest when $\mathcal{S}_{Z_\nu Z_\nu}(\omega^*)$ is maximized with respect to the correlation parameter (i.e., $b_\nu = \omega^* = 0$).

Comparison with simulations: The total variance of the population fluctuations given by local linearization is $\mathcal{C}_{xx}^{\text{ran}}(\tau=0) + \mathcal{C}_{xx}^{\text{dem}}(\tau=0)$. When $B(Z_\nu) = Z_\nu$ the model is linear, and it is no surprise that (2.18) and (2.22) give the same result as the exact calculation (the possibility of which was mentioned earlier). However, when $\nu = B(Z_\nu) = Z_\nu^2$ we have no exact analytic results, though we have derived the Normal approximation in Section 2.1. In equilibrium, the Normal approximation for the population variance reduces to

$$\lim_{t\to\infty}\text{var}[x] = [(\bar{Z}_\nu^2+\sigma_{Z_\nu}^2)/\mu_0] + 4\bar{Z}_\nu^2\sigma_{Z_\nu}^2/\left[\mu_0(b_\nu+\mu_0)\right]\,. \tag{2.24}$$

The second term in this expression is identical to $\mathcal{C}_{xx}^{\text{ran}}(\tau=0)$ (Eq. 2.22), and so the Normal approximation predicts the same response to the colour of the environmental noise as does local linearization. The first term in Eq. (2.24) differs from the local linear calculation $\mathcal{C}_{xx}^{\text{dem}}(\tau=0) = \bar{Z}_\nu^2/\mu_0$, in that the numerator is the correct mean ($\mathbf{E}[\nu] = \bar{Z}_\nu^2+\sigma_{Z_\nu}^2$). That the Normal approximation is thus superior is confirmed by Figure 3a, which compares both approximations with variances derived from simulation of the immigration-death process in equilibrium. This graph also demonstrates that the true system response to perturbation is maximized for $b_\nu \to 0$. Note also that the difference between the Normal and linear approximations is smallest in this limit where their common term is enhanced (i.e. for small b_ν).

Finally, Figure 3b compares Normal and local linear approximations to simulation results for the case $\nu = B(Z_\nu) = \exp\{Z_\nu\}$. The local linearization is less accurate here than in the previous case, but once again the predicted response to temporal correlations in the environment is qualitatively correct. Note that although both methods provide satisfactory results in equilibrium, only the Normal approximation can be applied to transient dynamics.

In summary, in the context of the immigration-death model we have shown how to formulate a stochastic population model, and write down forward equations describing its evolution. Some problems associated with modelling variability in the environment are discussed and several approaches suggested. Nonlinear models are found to be intractable to exact solution, a feature reflected in the problem of closure of the associated moment (or cumulant) evolution equations. Approximations based on cumulant truncation or distributional assumptions are introduced. In particular, the Normal approximation (where both approaches are equivalent) is applied to the immigration-death process in which stochastic environmental fluctuations are modelled by the mean-reverting Uhlenbeck-Ornstein process. This procedure is compared with another based on the linearization of a stochastic differential formulation of the model. Analytic and simulation results suggest that both approaches predict the correct response to the temporal correlation of the environmental noise, in addition to giving reasonable estimates of the size of the resultant fluctuations. In the remainder of this paper these techniques are applied to a multi-dimensional non-linear model of nematode infection of ruminants.

3 Helminth infection

Let $n_L(t)$ denote the number of free-living infective larval individuals in the area associated with one host animal, and $n_A(t)$ the number of adult parasites infecting a host. Transmission rates from larvae to host will naturally reflect the stocking density of the host animals, which in this model is fixed. In addition, we model the level of immunity to these parasites in the host population by some notional level, $n_r(t)$, which we consider discrete and non-negative. The model is identical to that formulated in Marion *et al.* (1998), except that here the transition rates are time-varying. In a small time interval $(t, t + \Delta t)$ the changes in the populations n_L, n_A and n_r are governed by the transition probabilities

$$Pr(n_L(t+\Delta t) = n_L(t)+1) = q(t)\lambda(r)n_A\Delta t \quad , \quad Pr(n_L(t+\Delta t) = n_L(t)-1) = (\beta(t)+\rho(t))n_L\Delta t$$
$$Pr(n_A(t+\Delta t) = n_A(t)+1) = \beta(t)p(n_r)n_L\Delta t \quad , \quad Pr(n_A(t+\Delta t) = n_A(t)-1) = \mu(n_r)n_A\Delta t$$
$$Pr(n_r(t+\Delta t) = n_r(t)+1) = \beta(t)n_L\Delta t \quad , \quad Pr(n_r(t+\Delta t) = n_r(t)-1) = \sigma n_r\Delta t. \qquad (3.1)$$

The probability that an egg develops to the free-living stage is $q(t)$, and $\rho(t)$ is the death rate of free-living stages. The probability of parasite establishment $p(n_r)$, and the rate of egg production $\lambda(n_r)$, are monotonic non-increasing functions, whilst the adult parasite mortality $\mu(n_r)$ is monotonic non-decreasing. The contact rate of infection is $\beta(t)$, and σ is the rate of loss of immunological memory. This model is a natural reformulation of the deterministic model with time-dependent rates proposed by Roberts and Grenfell (1992); the corresponding autonomous model was introduced in Roberts and Grenfell (1991). We restrict ourselves to the time-varying parameters considered by these authors, but in principle the methods described here can also be applied to variation in other model parameters.

3.1 Local linearization

Our first step is to re-cast this model in the form of Eq. (C.3); $\mathbf{x}(t)^T = (x_1, x_2, x_3)$ is the vector of continuous population variables corresponding to $\mathbf{n}^T = (n_L, n_A, n_r)$, with $\mathbf{u}^T = (\beta(t), q(t), \rho(t))$ the vector of time-varying parameters. The deterministic model is then defined by

$$\mathbf{f}(\mathbf{x}(t), \mathbf{u}(t)) = \frac{d}{dt} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix} = \begin{pmatrix} q(t)\lambda(x_3)x_2 - (\beta(t) + \rho(t))x_1 \\ \beta(t)p(x_3)x_1 - \mu(x_3)x_2 \\ \beta(t)x_1 - \sigma x_3 \end{pmatrix} ; \tag{3.2}$$

whilst the stochastic term is

$$\mathbf{g}(\mathbf{x}(t), \mathbf{u}(t), t) = \begin{pmatrix} [q(t)\lambda(x_3)x_2 + (\beta(t) + \rho(t))x_1]^{1/2}\gamma_L(t) \\ [\beta(t)p(x_3)x_1 + \mu(x_3)x_2]^{1/2}\gamma_A(t) \\ [\beta(t)x_1 + \sigma x_3]^{1/2}\gamma_r(t) \end{pmatrix} ,$$

where $(\gamma_L(t), \gamma_A(t), \gamma_r(t))$ is the time derivative of a three-dimensional Brownian motion. The steady state parameters are $\mathbf{u}_0^T = (\beta_0, q_0, \rho_0)$, and local linearization is applied around the fixed point of the deterministic dynamics $\mathbf{x}_1^T = (L_1, A_1, r_1)$, defined by $\mathbf{f}(\mathbf{x}, \mathbf{u}_0) = (0,0,0)^T$. The results of Section 2.2 are now applied to this system.

(i) Sinusoidal variation: Roberts and Grenfell (1992) consider the effects of applying sinusoidal perturbations, $A_j \cos(\omega_j t)$, to the model parameters β_0, q_0 and ρ_0 (e.g. $\beta(t) = \beta_0 + A_\beta \cos(\omega_\beta t)$), and here we outline some of their results. Applying Eq. (C.11), the magnitude of response in population l to unit sinusoidal perturbations in parameter u_j is found to be

$$|T(u_j, l, \omega_j)| \equiv |T_{lm}(\omega_j)| \, \partial f_m(\mathbf{x}_1, \mathbf{u}_0)/\partial u_j . \tag{3.3}$$

The *resonant frequency* of these perturbations is the ω_j which maximizes this response. Roberts and Grenfell (1992) then show that the system response to variation in ρ is proportional to that corresponding to q. Furthermore, for the parameter values of Table II the responses $|T(\beta, x_1, \omega)|/L_1$, $|T(\beta, x_2, \omega)|/A_1$ and $|T(q, x_2, \omega)|/A_1$ are visually indistinguishable from $|T(q, x_1, \omega)|/L_1$, and so it is sufficient to examine only the effect, in the free-living population x_1, of sinusoidal perturbations of q. The resonant frequencies of the system are found to be in the region of $\omega^* \approx 0.4046$ where $|T(q, x_1, \omega)|/L_1 \approx 500$, but for more realistic perturbations (of period one year) the system response is of a more reasonable level, $|T(q, x_1, \omega)|/L_1 \approx 1$. Numerical experiments support these conclusions.

(ii) Stochastic variation: We now focus on stochastic variation in the probability of egg development, $q(t)$. As in the immigration-death model (Section 2.1), assume that these fluctuations are modelled by a transformed mean-reverting Uhlenbeck-Ornstein process (*i.e.* $q(t) = B(Z_q(t))$). Recall that in the linearized regime the cross- and auto-correlations of the population fluctuations decompose into a sum of terms due to demographic and environmental fluctuations (see Eq. (C.14)). In the present case, the demographic terms are given by application of Eq. (C.17) employing the definitions (3.2), and since these calculations are described in some detail by Marion *et al.* (1998) we shall not consider them further here. Instead we focus on the environmental component given by expression (C.16), and consider only the response in the free-living population, whence

$$C_{n_L n_L}^{\text{ran}}(0) = \frac{1}{2\pi} \int_{-\infty}^{\infty} |T(q, n_L, \omega)|^2 \, \mathcal{S}_{Z_q Z_q}(\omega) d\omega . \tag{3.4}$$

Note that the spectral density of the mean-reverting Uhlenbeck-Ornstein process, Z_q, is $\mathcal{S}_{Z_q Z_q}(\omega) = 2b_q \sigma_{Z_q}/(\omega^2 + b_q^2)$. For $|T(q, n_L, \omega)|$ sufficiently peaked around the resonant frequency ω_*, the variance (3.4) can be approximated as

$$\mathcal{C}^{\mathrm{ran}}_{n_L n_L}(0) \approx \frac{1}{2\pi} |T(q, n_L, \omega_*)|^2 \, \mathcal{S}_{Z_q Z_q}(\omega_*) , \tag{3.5}$$

which is analogous to (2.23). This observation suggests that the shape of the system response to variations in the correlation parameter of the environmental noise (b_q) is proportional to $b_q/(\omega_*^2 + b_q^2)$ with a maximum at $b_q \approx \omega_*$. Thus, for the parameters of Table II the maximum response will occur at $b_q \approx 0.4046$, and direct evaluation of (3.4) shows this to be a reasonable approximation. In Section 4 we will compare the results of this linearization procedure with simulations of the full model for $q(t) = Z_\nu^2$. However, we first turn to the problem of closure, and the Normal approximation.

3.2 Normal approximation

(i) Deterministic parameter variability: In Marion *et al.* (1998) we consider the m.g.f. of the helminth process (3.1) in which there is no parameter variability. As in Section 2.1(ii), the forward equation for the m.g.f. is essentially unchanged for deterministically varying model parameters: time dependence of parameters is simply added. The derivation of moment equations is also unchanged, and, as for constant parameters, these equations are not closed and so one is forced to make some assumption regarding the higher-order terms. In Section 2.1 we see that one possibility is to assume that the process is Normally distributed, or, equivalently, that the cumulants of order three and above are zero. Assuming that $\lambda(n_r)$, $\mu(n_r)$ and $p(n_r)$ take the functional forms suggested in Table II, and excepting the time dependence of the model parameters, the system of equations obtained by applying the Normal approximation in this case is identical to that obtained for constant parameters in Marion *et al.* (1998) to which we refer the reader for a full derivation. The results of this procedure are compared with local linear approximation and simulation in Section 4.

(ii) Stochastic parameter variability: Now consider stochastic perturbations in the probability of egg development $q(t) = B_q(Z_q(t))$, and the contact rate $\beta(t) = B_\beta(Z_\beta(t))$. As earlier, we model these as transformations of the mean-reverting Uhlenbeck-Ornstein processes $Z_q(t)$ and $Z_\beta(t)$. We allow a fluctuating contact rate as this is the variable treated explicitly by the biologically motivated model considered in Section 5.

Following the argument presented in Appendix B, consider the Chapman-Kolmogorov forward equation for the joint density $p(n_L, n_A, n_r, Z_q, Z_\beta; t)$ where Z_q and Z_β are random walks in discrete time and space. Taking the continuous limit, which preserves finite instantaneous means and variances of $Z_q(t)$ and $Z_\beta(t)$, results in a forward equation for the process under continuous stochastic perturbation of the rate parameters. Introduction of the associated m.g.f. $M(\theta, \phi, \gamma, \psi_q, \psi_\beta) = \mathbf{E}\left[\exp\left\{\theta n_L(t) + \phi n_A(t) + \gamma n_r(t) + \psi_q Z_q(t) + \psi_\beta Z_\beta(t)\right\}\right]$ results in

$$
\begin{aligned}
\partial M/\partial t \;=\; & \lambda_0 (e^\theta - 1)\hat{B}_q(\partial/\partial \psi_q)\partial M(\theta, \phi, \gamma - \lambda_1, \psi_q, \psi_\beta; t)/\partial \phi \\
& + \; (e^{-\theta} - 1)(\hat{B}_\beta(\partial/\partial \psi_\beta)\partial M/\partial\theta + \rho\,\partial M/\partial\theta) \\
& + \; p(0)(e^\phi - 1)\hat{B}_\beta(\partial/\partial \psi_\beta)\partial M/\partial\theta + \mu(0)(e^{-\phi} - 1)\partial M/\partial\phi \\
& + \; (e^\gamma - 1)\hat{B}_\beta(\partial/\partial \psi_\beta)\partial M/\partial\theta + (e^{-\gamma} - 1)\sigma\partial M/\partial\gamma \\
& + \; b_\beta \psi_\beta \partial M/\partial \psi_\beta + (\sigma_\beta^2 \psi_\beta^2/2 + b_\beta \bar{Z}_\beta \psi_\beta)M + b_q \psi_q \partial M/\partial \psi_q + (\sigma_q^2 \psi_q^2/2 + b_q \bar{Z}_q \psi_q)M ,
\end{aligned}
\tag{3.6}
$$

where theˆnotation of Appendix B has been used (see Eq. B.5).

As an example, consider the case where $q(t)$ varies stochastically but where all other parameters are constant, that is $b_\beta = \sigma_\beta = 0$. As before, appropriate differentiation of Eq. (3.6) with respect to θ, ϕ,... leads to a set of moment evolution equations. The mean and variance of $Z_q(t)$ obey equations analogous to (B.7), whilst the remaining first- and second-order moments satisfy

$$
\begin{aligned}
d\mathbf{E}\left[n_L(t)\right]/dt &= \mathbf{E}\left[B_q(Z_q)n_A\lambda(n_r)\right] - (\beta+\rho)\mathbf{E}\left[n_L(t)\right], \\
d\mathbf{E}\left[n_A(t)\right]/dt &= p(0)\beta\mathbf{E}\left[n_L(t)\right] - \mu(0)\mathbf{E}\left[n_A(t)\right], \\
d\mathbf{E}\left[n_r(t)\right]/dt &= \beta\mathbf{E}\left[n_L(t)\right] - \sigma\mathbf{E}\left[n_r(t)\right], \\
d\mathbf{E}\left[n_L^2(t)\right]/dt &= (\beta+\rho)(\mathbf{E}\left[n_L(t)\right] - 2\mathbf{E}\left[n_L^2(t)\right]) \\
&\quad + (\mathbf{E}\left[B_q(Z_q)n_A\lambda(n_r)\right] + 2\mathbf{E}\left[B_q(Z_q)n_A n_L\lambda(n_r)\right]), \\
d\mathbf{E}\left[n_A^2(t)\right]/dt &= \beta p(0)(\mathbf{E}\left[n_L(t)\right] + 2\mathbf{E}\left[n_L n_A\right]) + \mu(0)(\mathbf{E}\left[n_A(t)\right] - 2\mathbf{E}\left[n_A^2(t)\right]), \\
d\mathbf{E}\left[n_r^2(t)\right]/dt &= \beta(\mathbf{E}\left[n_L(t)\right] + 2\mathbf{E}\left[n_L n_r\right]) + \sigma(\mathbf{E}\left[n_r(t)\right] - 2\mathbf{E}\left[n_r^2(t)\right]), \\
d\mathbf{E}\left[n_L n_A\right]/dt &= -(\beta+\rho+\mu(0))\mathbf{E}\left[n_L n_A\right] + \beta p(0)\mathbf{E}\left[n_L^2(t)\right] + \mathbf{E}\left[q n_A^2(t)\lambda(n_r)\right], \\
d\mathbf{E}\left[n_L n_r\right]/dt &= \beta\mathbf{E}\left[n_L^2(t)\right] - (\beta+\rho+\sigma)\mathbf{E}\left[n_L n_r\right] + \mathbf{E}\left[q n_A n_r\lambda(n_r)\right], \\
d\mathbf{E}\left[n_r n_A\right]/dt &= \beta\mathbf{E}\left[n_L n_A\right] - (\sigma+\mu(0))\mathbf{E}\left[n_r n_A\right] + \beta p\mathbf{E}\left[n_L n_r\right], \\
d\mathbf{E}\left[n_L Z_q\right]/dt &= -b_q(\mathbf{E}\left[n_L Z_q\right] - \bar{Z}_q\mathbf{E}\left[n_L(t)\right]) + \mathbf{E}\left[n_A B_q(Z_q)Z_q n_r\lambda(n_r)\right] - (\beta+\rho)\mathbf{E}\left[n_A Z_q\right], \\
d\mathbf{E}\left[n_A Z_q\right]/dt &= -b_q(\mathbf{E}\left[n_A Z_q\right] - \bar{Z}_q\mathbf{E}\left[n_A(t)\right]) + \beta p(0)\mathbf{E}\left[n_L Z_q\right] - \mu(0)\mathbf{E}\left[n_A Z_q\right], \\
d\mathbf{E}\left[n_r Z_q\right]/dt &= -b_q(\mathbf{E}\left[n_r Z_q\right] - \bar{Z}_q\mathbf{E}\left[n_r(t)\right]) + \beta\mathbf{E}\left[n_L Z_q\right] - \sigma\mathbf{E}\left[n_r Z_q\right].
\end{aligned}
$$

As in the non-autonomous system (Marion *et al.*, 1998), this set of equations is not closed, but depends on an infinite series of higher-order moments through expectations such as $\mathbf{E}\left[B_q(Z_q)n_A\lambda(n_r)\right]$. Paralleling Section 2.1 we employ second-order cumulant truncation. Let $\mathbf{x}^T = (n_L, n_A, n_r, Z_q)$ with expectation $\bar{\mathbf{x}} = \mathbf{E}\left[\mathbf{x}\right]$ and variance-covariance matrix $\Sigma = \mathbf{E}\left[(\mathbf{x}-\bar{\mathbf{x}})^T(\mathbf{x}-\bar{\mathbf{x}})\right]$. Then for $\mathbf{w}^T = (w_1, w_2, w_3, w_4)$, the c.g.f. for the truncated process is $K_2(\mathbf{w}) = \mathbf{w}^T\bar{\mathbf{x}} + \frac{1}{2}\mathbf{w}^T\Sigma\mathbf{w}$, and approximations to expressions such as $\mathbf{E}\left[B_q(Z_q)n_A\lambda(n_r)\right]$ can be obtained via the associated m.g.f.

$$
M_2(\mathbf{w}) = \exp\left(K_2(\mathbf{w})\right) \approx \mathbf{E}\left[\exp\left\{w_1 n_L + w_2 n_A + w_3 n_r + w_4 Z_q\right\}\right]. \tag{3.7}
$$

It is clear that this procedure is possible for a wide range of transformations $B_q(Z_q)$, including $B_q(Z_q) = Z_q^2$ and $B_q(Z_q) = \exp\{Z_q\}$. Normal approximations to the moment update equations can be obtained for alternative scenarios in a similar fashion. For example, in Section 5 we apply the above techniques to the case where only $\beta(t) = B_\beta(Z_q)$ is perturbed by a continuous stochastic process. Other possible extensions include employing more general processes in place of Z_q.

4 Simulation in the endemic regime

The endemic regime corresponds to the fixed point of the deterministic system with constant parameters, and, in the stochastic model, to fluctuations around this point. We compare local linearization and the Normal approximation with the results of simulation, and consider both deterministic and stochastic variation of the probability in egg development.

Deterministic time dependence of model parameters means that no steady-state solution exists. However, Figure 4 depicts the Normal approximation to $\mathbf{E}[n_L] \pm \sigma_L$ and a time series generated

from the full stochastic process for $q(t) = q_0[1 + \sin(2\pi t)]$. Empirical observations reported in Roberts and Grenfell (1992) confirm that this perturbation is biologically reasonable. The Normal approximation appears to predict the fluctuations reasonably well, though it breaks down at $t \approx 34$ years (not shown). This is a reflection of the magnitude of fluctuations around q_0. Figure 4 clearly shows fluctuations from the endemic equilibrium $L_1 = 78847$ greater than $10 \times L_1$, in clear conflict with the magnitude of approximately L_1 (*i.e.* $|T(q, n_L, \omega)|/L_1 \approx 1$) predicted by the linearization of Section 3.1. However, it should be noted that this is a purely transitory response, and the linear prediction is correct for large time.

Now consider the stochastic case $q(t) = B_q(Z_q(t)) = Z_q^2$, where, as before, $Z_q(t)$ is a mean-reverting Uhlenbeck-Ornstein process. We assume that $\mathbf{E}[q] = 0.35$ corresponding to the steady-state value given in Table II, and that the other parameters remain as stated there. For a given variance, $\text{var}[q]$, the parameters $\bar{Z}_q$ and σ_q describing $Z_q(t)$ are given by application of equations analogous to (2.9). This process implies a choice of the correlation parameter b_q, but we will consider representative values. Table III shows the standard deviation of fluctuations in the free-living population, σ_L, derived from a long simulation over $t = 0, ..., 5000$ years in the endemic regime. The approximations to this quantity derived from the Normal and local approximations are also shown. Both methods predict the correct magnitude of response. Note also that the value of b_q has a significant impact on the magnitude of σ_L. For a given $\text{var}[q]$ this response is increased considerably as we move towards $b_q = \omega^* \approx 0.4046$. This prediction of local linearization is also supported by the Normal approximation, which for $\text{var}[q] = 10^{-7}$ has a maximum σ_L for $b_q \in (0.40457, 0.4046)$. However, for fluctuations much larger than this the Normal approximation breaks down. This is the reason for the missing figure in Table III. Recall that we witnessed a similar, but less extreme, breakdown of the Normal approximation in Section 2.1 (see Figure 2).

For environmental variances greater than those examined in Table III we find that stochastic fluctuation around the endemic equilibrium frequently results in extinction. Table IV shows some results pertaining to this. Here the population fluctuations are large, and the Normal approximation is unhelpful. In most cases it breaks down, and where it does not it seems to underestimate the fluctuations. In contrast the local linear approximation appears to be rather robust. Comparison with simulations suggests that variances predicted by local linearization can be used to provide estimates of the extinction risk. Note also that the resonant frequency effect can be seen clearly, with the percentage of runs ending in extinction associated with $\text{var}[q] = 10^{-4}$ ($b_q = 0.5$) being considerably greater than that associated with the larger variance $\text{var}[q] = 10^{-3}$ ($b_q = 50$). We note that in the context of discrete time models, Halley and Iwasa (1998) investigate extinction risk in the presence of white environmental noise, whilst Johst and Wissel (1997) demonstrate the importance of correlation in environmental fluctuations for extinction risk.

5 A more realistic environmental perturbation

So far we have explored the effects of theoretical perturbations and time-dependencies of the rate parameters. However, Beecham (1997) has investigated the effects of micro-climatic fluctuations on the behaviour of free-living nematodes within grass swards. The resultant vertical movements of the parasites cause variations in the numbers ingested by hosts, resulting in weather-driven fluctuations in the contact rate β. In this section we make use of a time series of daily values of the contact rate,

$\widetilde{\beta}(t)$ (Beecham, 1997). Note that for fractions of a day one must interpolate between daily values when using $\widetilde{\beta}(t)$ in simulations.

The length of this series is limited to fourteen years by the available weather data, with the first year shown in Figure 5. As can be seen, the fluctuations in the contact rate are large. The periods where $\widetilde{\beta}(t)$ is zero reflect a management regime where the hosts are removed from the pasture between day 300 of one year and the 51st day of the following year. Roberts and Grenfell (1991, 1992) consider a management scenario in which hosts are removed at the end of each year and replaced by individuals with no acquired immunity. Marion *et al.* (1998) demonstrate that, for constant rate parameters, the stochastic effects are negligible in this case (see Section 5). Here we combine both management models, assuming that hosts have no acquired immunity when they return to pasture after the period of absence. In this case, without environmental fluctuations the deterministic model still provides a highly accurate representation of the population dynamics. However, Figure 5b shows that the effect on the population dynamics of these weather driven fluctuations in the contact rate is considerable.

Our first attempt to predict uncertainty in model output resulting from fluctuations in the contact rate involved re-sampling from the existing time series $\widetilde{\beta}$. However, this did not yield satisfactory results and will not be considered further. Our second approach was to produce realistic stochastic models of the fluctuations $\widetilde{\beta}$, and we now describe two such models. Using ARIMA processes (Box and Jenkins, 1970) a good fit is obtained by modelling the square root of the contact rate using a third-order auto-regressive process. Figure 6a shows the result of applying this model of $\widetilde{\beta}(t)$ in simulations of the helminth process. The approach seems to work reasonably well, but fluctuations between yearly peak values are slightly greater than those associated with $\widetilde{\beta}(t)$ itself. A large number of simulations could be used to obtain confidence intervals of the population fluctuations, though this may be computationally expensive. ARIMA processes are flexible models for environmental perturbations, but so far we have been unable to incorporate them into the theoretical approximations derived earlier. We therefore consider models of $\widetilde{\beta}(t)$ based on the mean-reverting Uhlenbeck-Ornstein process, which itself can be regarded as a continuous limit of a first-order auto-regressive process. This allows us to calculate approximate confidence intervals for the population fluctuations.

Using expressions analogous to (2.9), a mean-reverting Uhlenbeck-Ornstein process is fitted to the square root of $\widetilde{\beta}$ (that is, $\beta = Z_\beta(t)^2$). As noted, this procedure leaves the correlation parameter b_β to be determined. One possible approach is to fit, by least squares, the spectral density of $Z_\beta(t)$ to that of $\sqrt{\widetilde{\beta}(t)}$, though this yields a highly correlated time series (small b_β) at odds with that shown in Figure 5a. Furthermore, when this is used in simulations, the resultant population fluctuations are dissimilar to those of Figure 5b. Instead, we vary the correlation parameter b_β until the population fluctuations qualitatively resemble those obtained when using $\widetilde{\beta}$ directly. A reasonable value is found to be $b_\beta = 200$, and the resulting population fluctuations are shown in Figure 6b.

As noted in Section 3.2, the Normal approximation can be derived from Eq. (3.6) with $b_q = \sigma_q = 0$. The result is a set of equations analogous to (3.7), describing the case where $\beta = B_\beta(Z_\beta)$. The resultant Normal approximation, when $\beta = Z_\beta^2$ is fitted to $\widetilde{\beta}$ and $b_\beta = 200$, is shown in Figure 7a. The fluctuations in the free-living larval population $n_L(t)$ are shown alongside Normal

approximations to the expected value $\mathbf{E}\left[n_L(t)\right]$ together with the ± 2 standard deviation interval. The approximation appears reasonable since the population fluctuations, derived from simulation with $\beta = Z_{\tilde{\beta}}^2$, are contained within the confidence intervals more than 96% of the time (based on one observation every second day for 14 years). How useful is this analytic approximation in describing the likely population fluctuations resulting from the weather driven contact rate $\widetilde{\beta}$ itself? The results shown in Figure 7b are clearly encouraging, though, using the same frequency of observation over 14 years, the population fluctuations (based on simulation with contact rate $\widetilde{\beta}$ itself) lie outside the approximate ± 2 standard deviation interval more than 15% of the time. However, this figure may not be significant since successive observations of the model output are highly correlated. Thus in summary, the Normal approximation gives some guide to the extent of the expected population fluctuations. Improvements should result from using more realistic distributional assumptions, and more flexible, but analytically tractable, models for environmental variation. We hope to address both issues in subsequent publications.

6 Discussion

We have considered the problem of environmental and parameter variation in stochastic population models. We find that deterministic and discrete stochastic parameter variation present few new problems in terms of analytic approximation and simulation of the process. In contrast, care is needed in introducing continuous stochastic parameter variation. A continuous limit of a simple random walk is derived and a special case, the mean-reverting Uhlenbeck-Ornstein process, is used as a prototype model for environmental stochasticity. This process has an exponentially decaying temporal correlation structure, and it would be interesting to study more general perturbations.

Simulation and analytic treatment of stochastic population models in the presence of environmental variation are introduced using the immigration-death process as an example. In the context of plausible models of continuous stochastic parameter variation, even this process is found to be analytically intractable; analytical approximations considered are the Normal approximation and local linearization of a stochastic differential formulation of the model. These approximations are evaluated using extensive numerical simulation, and although the Normal approximation is more flexible and slightly more accurate, both methods predict the correct response to temporal correlations in parameter fluctuations.

These techniques are subsequently applied to a model of nematode infection in ruminants, which is analytically intractable at present, and computationally more demanding than the immigration-death process. In the endemic regime, following the deterministic analysis of Roberts and Grenfell (1992), sinusoidal perturbations in the probability of egg development q are considered. The Normal approximation accurately reflects the simulated population fluctuations, whilst the linearized deterministic analysis underestimates the transient system response. Continuous stochastic perturbations in q are also examined in the endemic regime. As the variance of these parameter fluctuations grows, the resultant population fluctuations are increasingly likely to result in extinction. Unfortunately, the Normal approximation breaks down in this regime, but local linearization provides a good indication of extinction risk. A key factor in determining the size of resultant population fluctuations, and thus the extent of this risk, is the temporal correlation of the perturbing process: both the Normal and local linear approximations predict the system response to changes

in the strength of this correlation. It should be noted that the helminth model was chosen as a case study. In reality the infection is unlikely to die out spontaneously and the extinctions predicted may suggest inadequacies in the model. Perhaps the most striking of these is that only one host is considered, and it is likely that heterogeneity in host response to infection may result in greater stability (Anderson and May, 1978).

Finally, a time series of fluctuations in the contact rate of the infection, derived from a mechanistic model of helminth response to micro-climatic fluctuations, is studied. These fluctuations give rise to marked stochastic effects in a managed regime, effects which are negligible in the absence of environmental stochasticity. The limited length of the time series prompted the search for simple stochastic models of fluctuations in the contact rate. Whilst an adequate auto-regressive model was identified, its analytic intractability and computational cost presented barriers to the evaluation of the fluctuation characteristics of the population. This led to the use of a suitably parametrised transformed mean-reverting Uhlenbeck-Ornstein process, for which approximate, but reasonably accurate variances can be derived from the Normal approximation. These results may be improved: (i), by using more appropriate distributional assumptions; and (ii), by developing more general, but analytically tractable, parameter perturbations.

Environmental fluctuations play a crucial role in realistic population models in biology. Our studies with a plausible model for helminth infection in ruminants suggests that in this context they are more significant than demographic stochasticity. In addition, the correlation structure, or colour, of environmental stochasticity is crucial in determining the resultant population fluctuations; this effect can be related to a resonant frequency of the linearized system. In this paper we have presented an important set of quantitative methods for assessing the population variability associated with both environmental and demographic stochasticity. This methodology is applicable to a wide range of spatial and non-spatial population models in continuous time, and allows for a simple correlation structure in the environmental fluctuations. Whilst these techniques are approximate, simulation results from a multi-dimensional nonlinear model suggest they accurately predict the magnitude of population fluctuations and the appropriate response to changes in the colour of environmental noise.

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Appendix A: Deterministic variation

Application of the auxiliary equations to expression (2.6) gives rise to the solution

$$K(\theta;t) - U \int_0^t \nu(w)\exp\left[\int_0^w \mu(y)dy\right]dw = \psi(U) \quad \text{with} \quad U = \left(1 - e^\theta\right)\exp\left[-\int_0^t \mu(w)dw\right], \text{ (A.1)}$$

where $\psi(U)$ is an arbitrary function determined by the boundary conditions. A closed form solution is possible when the death rate is constant, *i.e.* $\mu(t) = \mu$, and the immigration rate varies sinusoidally, *i.e.* $\nu(t) = \nu_0\left[1 + \epsilon\cos(\omega t + \phi)\right]$. Then

$$K(\theta;t) = K_0(\theta;t) - \epsilon\nu_0(1 - e^\theta)\left[f(t) - f(0)e^{-\mu t}\right] \tag{A.2}$$

where $f(t) = \left[\mu\cos(\omega t + \phi) + \omega\sin(\omega t + \phi)\right]/(\mu^2 + \omega^2)$, and K_0, the c.g.f. for constant immigration and death rates, is given by (2.4). Repeated differentiation of (A.2) with respect to θ (at $\theta = 0$) shows that the corresponding cumulants are those for the time-homogeneous case plus the oscillating component $\epsilon\nu_0\left[f(t) - f(0)e^{-\mu t}\right]$. Rewriting (A.2) in terms of the m.g.f., and substituting $\theta = \ln z$, gives the probability generating function (p.g.f.) $G(z;t) \equiv \Sigma_{n=0}^\infty p(n;t)z^n$. Thus $p(n;t)$ is the coefficient of z^n in the expansion of $G(z;t)$; in particular, the probability of zero population size at time t is $p(0;t) = G(0;t)$. Note that if $n_0 = 0$ then $n(t)$ follows a Poisson distribution with rate $\rho = \epsilon\nu(0)[f(t) - f(0)e^{-\mu t}] + \nu_0(1 - e^{-\mu t})/\mu$.

Appendix B: Continuous stochastic variation

In this appendix we show one possible description of continuous stochastic variation in model parameters. Once again consider the immigration-death model, but let us now assume that the rates take the form $\mu(t) = D(Z_\mu(t))$ and $\nu(t) = B(Z_\nu(t))$, where the perturbing processes $Z_\mu(t)$ and $Z_\nu(t)$ are Markov chains. Here $Z_\nu(t)$ changes in increments of size $\pm \Delta Z$ at fixed time steps Δt according to the probabilities

$$P(Z_\nu(t + \Delta t) = Z_\nu(t) + \Delta Z) = \theta_\nu \qquad \text{and} \qquad P(Z_\nu(t + \Delta t) = Z_\nu(t) - \Delta Z) = \phi_\nu \,, \qquad \text{(B.1)}$$

with analogous expressions for $Z_\mu(t)$. It is straightforward to write down the forward equation for the full process $\{p(x, Z_\nu, Z_\mu; t)\}$ by considering the possible changes occurring at discrete intervals Δt apart, just as before. If care is observed in taking the limits $\Delta t, \Delta Z \to 0$ then a mixed discrete-continuous process (and associated forward equation) can also be obtained. This requires the existence of the instantaneous means and variances of the perturbing processes, namely

$$\lim_{\Delta t, \Delta Z \to 0} \mathbf{E}\left[Z_\nu(t + \Delta t) - Z_\nu(t)\right]/\Delta t = \lim_{\Delta t, \Delta Z \to 0} \Delta Z(\theta_\nu - \phi_\nu)/\Delta t = \beta_\nu(Z, t) \,, \qquad \text{(B.2)}$$

$$\lim_{\Delta t, \Delta Z \to 0} \text{var}\left[Z_\nu(t + \Delta t) - Z_\nu(t)\right]/\Delta t = \lim_{\Delta t, \Delta Z \to 0} (\Delta Z)^2(\theta_\nu + \phi_\nu - (\theta_\nu - \phi_\nu)^2)/\Delta t = \alpha_\nu(Z, t) \,,$$

for the process perturbing ν; we use analogous limits $\beta_\mu(Z, t)$ and $\alpha_\mu(Z, t)$ for the process perturbing μ. In the case where the transition probabilities are constant, the successive increments $Z_\nu(t + \Delta t) - Z_\nu(t)$ are independent random variables, and conditions (B.2) are equivalent to requiring the unit time mean and variance of $Z_\nu(t)$ to be finite. It is straightforward to show (see Cox and Miller, 1965, p. 213-215) that if the limits (B.2) are to exist we require

$$\theta_\nu = \frac{1}{2A}\left(\alpha_\nu + \beta_\nu \Delta Z\right) \qquad \text{and} \qquad \phi_\nu = \frac{1}{2A}\left(\alpha_\nu - \beta_\nu \Delta Z\right) \,, \qquad \text{(B.3)}$$

where $\Delta Z^2 = A \Delta t$ for some constant $A > \alpha_\nu$. Analogous expressions also hold for the process $Z_\mu(t)$. On taking the continuous limit and applying these conditions we obtain the following Kolmogorov forward equation for the joint density $p(n, Z_\nu, Z_\mu; t)$ of the immigration-death process with the environmental noise, namely

$$\begin{aligned} \partial p/\partial t = {}& B(Z_\nu)p(n - 1, Z_\nu, Z_\mu; t) + (n + 1)D(Z_\mu)p(n + 1, Z_\nu, Z_\mu; t) \qquad \text{(B.4)} \\ & - \left[nD(Z_\mu) + B(Z_\nu)\right]p + \partial^2[\alpha_\mu p]/\partial\mu^2 - \partial[\beta_\mu p]/\partial\mu + \partial^2[\alpha_\nu p]/\partial\nu^2 - \partial[\beta_\nu p]/\partial\nu \,. \end{aligned}$$

(Here p has been used as shorthand for $p(n, Z_\nu, Z_\mu; t)$). In the case where $\alpha_\mu = \alpha_\nu = \beta_\mu = \beta_\nu = 0$, upon noting that $\nu = B(Z_\nu)$ and $\mu = D(Z_\mu)$ we recover the forward equation (2.2) for the immigration-death model with constant rate parameters. Introducing the moment generating function $M(\theta, \lambda_\nu, \lambda_\mu; t) = \mathbf{E}\left[\exp\{n\theta + Z_\nu\lambda_\nu + Z_\mu\lambda_\mu\}\right]$ now yields

$$\begin{aligned} \partial M/\partial t = {}& (e^\theta - 1)\hat{B}(\partial/\partial\lambda_\nu)M + (e^{-\theta} - 1)\hat{D}(\partial/\partial\lambda_\mu)\partial M/\partial\theta + \lambda_\nu^2\hat{\alpha}_\nu(\partial/\partial\lambda_\nu)M/2 \\ & + \lambda_\nu\hat{\beta}_\nu(\partial/\partial\lambda_\nu)M + \lambda_\mu^2\hat{\alpha}_\mu(\partial/\partial\lambda_\mu)M/2 + \lambda_\mu\hat{\beta}_\mu(\partial/\partial\lambda_\mu)M \,. \end{aligned} \qquad \text{(B.5)}$$

(The $\hat{}$ notation means that, for example, if $B(x) = a\,x + b\,x^2$, then $\hat{B}(\partial/\partial\lambda_\nu)M = a\,\partial M/\partial\lambda_\nu + b\,\partial^2 M/\partial\lambda_\nu^2$).

Simple models of environmental stochasticity

On assuming $\hat{B} = \hat{D} = \hat{\alpha}_\mu = \hat{\beta}_\mu = 0$, we reduce (B.5) to the forward equation

$$\partial M(\lambda_\nu; t)/\partial t = \lambda_\nu^2 \hat{\alpha}_\nu (\partial/\partial \lambda_\nu) M/2 + \lambda_\nu \hat{\beta}_\nu (\partial/\partial \lambda_\nu) M \,, \tag{B.6}$$

which describes the evolution of Z_ν only. When $\alpha_\nu = \sigma_\nu^2$ and $\beta_\nu = b_\nu$, Cox and Miller (1965, p. 206) solve Eq. (B.6) to find the cumulant generating function $K(\lambda_\nu; t) \equiv \ln M(\lambda_\nu; t) = (b_\nu \lambda_\nu + \lambda_\nu^2 \sigma_\nu^2/2)t$. Thus $Z_\nu(t)$, a *Wiener process with drift*, is Normally distributed with mean $(b_\nu t)$ and variance $(\sigma_\nu^2 t)$, both of which diverge linearly with time. Clearly this can be a credible model for environmental variability only over a short time scale. However, on re-writing $\beta_\nu = b_\nu[\bar{Z}_\nu - Z_\nu(t)]$, $Z_\nu(t)$ follows a *mean-reverting Uhlenbeck-Ornstein velocity process* (Mao, 1997) which is Normally distributed with mean and variance (see Cox and Miller, 1965, p. 225)

$$\mathbf{E}\left[Z_\nu(t)\right] = \bar{Z}_\nu + (Z_\nu(0) - \bar{Z}_\nu)e^{-b_\nu t} \quad \text{and} \quad \text{var}(Z_\nu(t)) = \sigma_\nu^2 \left(1 - e^{-2b_\nu t}\right)/2b_\nu \,. \tag{B.7}$$

Thus in equilibrium the mean and variance are $\bar{Z}_\nu$ and $\sigma_\nu^2/2b_\nu$, respectively. In what follows we will take this equilibrium process to be our basic model of environmental variability. Note one could consider many alternative forms, for instance $\hat{\alpha}_\nu \propto Z_\nu$ produces a geometric Brownian process (Mao, 1997). However, the mean-reverting Uhlenbeck-Ornstein velocity process and its transformations provide a rich family of models for environmental perturbations.

Appendix C: Stochastic differential equations

Consider the general case with k interacting populations $\mathbf{n}^T = (n_1, n_2,..., n_k)$, and p parameters $\mathbf{u}(t)^T = (u_1(t), u_2(t), ..., u_p(t))$. Given the transition probabilities $P(n_j(t + \Delta t) = n_j(t) - 1)$, ..., the mean and variance of the update $n_j(t + \Delta t) - n_j(t)$ are respectively

$$f_j(\mathbf{n}, \mathbf{u}(t))\Delta t \equiv (+1)\Pr(n_j(t + \Delta t) = n_j(t) + 1) + (-1)P(n_j(t + \Delta t) = n_j(t) - 1)\,, \tag{C.1}$$
$$q_j(\mathbf{n}, \mathbf{u}(t))\Delta t \equiv (+1)^2 \Pr(n_j(t + \Delta t) = n_j(t) + 1) + (-1)^2 \Pr(n_j(t + \Delta t) = n_j(t) - 1)\,.$$

Now $\mathbf{x}^T = (x_1, x_2, ..., x_k)$ are the continuous-valued variables corresponding to $\mathbf{n}$, and the change in population j during the interval $(t, t + \Delta t)$ is

$$\Delta x_j(t) = x_j(t + \delta t) - x_j(t) = f_j(\mathbf{n}, \mathbf{u}(t))\Delta t + q_j^{1/2}(\mathbf{x})\Delta t^{1/2}\eta_j(t)\,, \tag{C.2}$$

where $\{\eta_j(t)\}$ is a white noise process of zero mean and unit variance. Note that interpreting (C.2) as a difference equation allows the immediate simulation of the process $x(t)$; indeed, this was the method adopted for the mean-reverting Uhlenbeck-Ornstein process in Eq. (2.14). Dividing Eq. (C.2) through by Δt and taking the limit $\Delta t \to 0$ leads to a set of s.d.e's which, in matrix notation, can be written as

$$d\mathbf{x}(t)/dt = \mathbf{f}(\mathbf{x}(t), \mathbf{u}(t)) + \mathbf{g}(\mathbf{x}(t), \mathbf{u}(t))\,, \tag{C.3}$$

where $\mathbf{f}(\mathbf{x}(t), \mathbf{u}(t))^T = (f_1, f_2, ..., f_k)$ and $\mathbf{g}(\mathbf{x}(t), \mathbf{u}(t))^T = (q_1^{1/2}\gamma_1(t), ..., q_n^{1/2}\gamma_n(t))$; $\gamma_i(t) = \lim_{\Delta t \to 0} \eta(t)/dt^{1/2}$ are time derivatives of Weiner processes with zero mean and unit variance at unit time.

At present no general solution exists for s.d.e's of the form (C.3) (see Mao, 1997), though progress can be made by linearization. Assume that the parameters are of the form $\mathbf{u}(t) = \mathbf{u}_0 + \delta\mathbf{u}(t)$, where

the deviations δu_i of individual components, $u_i(t)$, from some constant level $(u_0)_i$ are small. If $dx/dt = f(\mathbf{x}, \mathbf{u}_0)$ has a fixed point $\mathbf{x}_1$, then in the limit of large t (where the transient solution can be ignored), and for small deviations $\mathbf{v}(t)$ from $\mathbf{x}_1$ (*i.e.* $\mathbf{x}(t) = \mathbf{x}_1 + \mathbf{v}(t)$), Eq. (C.3) can be linearized to give

$$\frac{d\mathbf{v}(t)}{dt} = \mathbf{v}(t)\frac{\partial \mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)}{\partial \mathbf{x}} + \sum_{j=1}^{p} \delta u_j \frac{\partial \mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)}{\partial u_j} + \mathbf{g}(\mathbf{x}_1, \mathbf{u}_0, t)\,. \tag{C.4}$$

A standard stability analysis of the linearized deterministic system reveals the behaviour of the transient solution. Such an analysis is conducted by Roberts and Grenfell (1991) for a model of nematodiasis. One way to solve Eq. (C.4) is to make use of the Fourier transformation

$$\widetilde{h}(\omega) = \int_{-\infty}^{\infty} h(t)e^{-i\omega t}dt\,, \tag{C.5}$$

and its inverse $h(t) = \int_{-\infty}^{\infty} \widetilde{h}(\omega)e^{i\omega t}d\omega/2\pi$. A useful property of this transformation is its linearization of the time derivative (*i.e.* $d\widetilde{h}(\omega)/dt = i\omega\widetilde{h}(\omega)$). For $t < 0$, define $\mathbf{v}(t)^T = \mathbf{g}(\mathbf{x}_1, \mathbf{u}_0, t)^T = (0, 0, ..., 0)$. Then on applying the Fourier transformation to (C.4) we obtain

$$i\omega\widetilde{\mathbf{v}}(\omega) = \widetilde{\mathbf{v}}(\omega)\frac{\partial \mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)}{\partial \mathbf{x}} + \sum_{j=1}^{p} \delta\widetilde{u}_j(\omega)\frac{\partial \mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)}{\partial u_j} + \widetilde{\mathbf{g}}(\mathbf{x}_1, \mathbf{u}_0, \omega)\,. \tag{C.6}$$

Collecting terms involving $\widetilde{\mathbf{v}}(\omega)$ and multiplying by the *transfer function* matrix

$$\mathbf{T}(\omega) = [i\omega\mathbf{I}_k - \partial\mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)/\partial\mathbf{x}]^{-1} \tag{C.7}$$

($\mathbf{I}_k$ being the $k \times k$ identity matrix) yields

$$\widetilde{\mathbf{v}}(\omega) = \mathbf{T}(\omega)\left[\sum_{j=1}^{p} \delta\widetilde{u}_j(\omega)\frac{\partial\mathbf{f}(\mathbf{x}_1, \mathbf{u}_0)}{\partial u_j} + \widetilde{\mathbf{g}}(\mathbf{x}_1, \mathbf{u}_0, \omega)\right]\,. \tag{C.8}$$

The first term on the right-hand side of (C.8) is attributable to environmental (*i.e.* parameter) fluctuations, whilst the second is due to demographic stochasticity. Taking the inverse Fourier transformation of $\widetilde{\mathbf{v}}(\omega)$ gives

$$\mathbf{v}(t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} \widetilde{\mathbf{v}}(\omega)e^{i\omega t}d\omega\,. \tag{C.9}$$

As a further refinement, assume that the perturbation of the model parameters can be written as the sum of a deterministic and a stochastic term, that is $\mathbf{u}(t) = \mathbf{u}_0 + \delta\mathbf{d}(t) + \delta\mathbf{r}(t)$. This naturally leads to the decomposition

$$\mathbf{v}(t) = \mathbf{v}^{\text{det}}(t) + \mathbf{v}^{\text{ran}}(t) + \mathbf{v}^{\text{dem}}(t)\,. \tag{C.10}$$

Since the white noise which drives the demographic fluctuations has zero mean, we have $\mathbf{E}[\mathbf{v}^{\text{dem}}(t)] = 0$. Let the deterministic component, $\delta\mathbf{d}(t)$, account for any expected displacement from $\mathbf{u}_0$, and assume that $\mathbf{E}[\delta\mathbf{r}(t)] = 0$, so that $\mathbf{E}[\mathbf{v}^{\text{ran}}(t)] = 0$. Then we need only consider $\mathbf{E}[\mathbf{v}^{\text{det}}(t)]$. Noting that a wide range of perturbations can be expressed in terms of Fourier series of sinusoidal terms, we consider the deterministic perturbation $\delta d_j(t) = A_j\cos(\omega_j t + \phi_j)$. Since the Fourier transform of

$A_j \cos(\omega_j t + \phi_j)$ is $A_j \pi \left[\exp(i\phi) \delta(\omega_j - \omega) + \exp(-i\phi) \delta(\omega_j + \omega) \right]$, where $\delta(\cdot)$ denotes the Dirac delta function, it follows that

$$\mathbf{E}\left[v_l(t)\right] = \sum_{j=1}^{p} \sum_{m=1}^{k} |T_{lm}(\omega_j)| \frac{\partial f_m(\mathbf{x}_1, \mathbf{u}_0)}{\partial u_j} A_j \cos(\omega_j t + \phi_j + \xi_{lm}(\omega_j)), \tag{C.11}$$

where the phase shift is

$$\tan(\xi_{lm}(\omega_j)) = \Im[T_{lm}(\omega_j)] / \Re[T_{lm}(\omega_j)], \tag{C.12}$$

and $\Re[..]$ and $\Im[..]$ denote real and imaginary parts (see Nisbet and Gurney, 1982, p. 37). The deterministic population fluctuations $\mathbf{E}\left[x_l(t)\right] = (\mathbf{x}_1)_l + \mathbf{E}\left[v_l(t)\right]$ are thus of the same frequency as the environmental perturbation, but the magnitude and phase, determined by the transfer function matrix $\mathbf{T}(\omega)$, are different.

Let us now consider the second-order fluctuation characteristics, namely the time-lagged auto- and cross-correlations defined by

$$\mathcal{C}_{x_l x_m}(\tau) = \mathbf{E_t}\left[\{v_l(t) - \mathbf{E_t}\left[v_l\right]\}\{v_m(t + \tau) - \mathbf{E_t}\left[v_m\right]\} \right], \tag{C.13}$$

where the time average $\mathbf{E_t}\left[g(t)\right] = \lim_{T \to \infty}(1/T) \int_0^T g(t)dt$. In general, $\mathcal{C}_{x_l x_m}(\tau)$ can be calculated directly from the linear solution (C.9), and when $\tau = 0$ this corresponds to population variances and covariances. Furthermore, if we make the (not unreasonable) assumption that the white noise process driving the demographic fluctuations and the stochastic environmental perturbations of different parameters are independent, both of one another and of the deterministic environmental fluctuations, we find

$$\mathcal{C}_{x_l x_m}(\tau) = \mathcal{C}_{x_l x_m}^{\text{det}}(\tau) + \mathcal{C}_{x_l x_m}^{\text{ran}}(\tau) + \mathcal{C}_{x_l x_m}^{\text{dem}}(\tau). \tag{C.14}$$

Thus, as with the fluctuations $\mathbf{v}(t)$ themselves (see Eq. C.10), the total time-lagged covariance can be decomposed into terms due to deterministic environmental fluctuations, and demographic and environmental stochasticity. Whilst this reflects Rand and Wilson's (1991) partition of stochasticity into demographic and environmental components, it is important to realize that this additive property is a result of the linearization procedure, in addition to the independence of the fluctuating terms. Assuming sinusoidal deterministic environmental fluctuations, $\delta d_a(t) = A_a \cos(\omega_a t + \phi_a)$, we find

$$
\begin{aligned}
\mathcal{C}_{x_l x_m}^{\text{det}}(\tau) &= \mathbf{E_t}[\{v_l^{\text{det}}(t) - \mathbf{E_t}[v_l^{\text{det}}]\}\{v_m^{\text{det}}(t+\tau) - \mathbf{E_t}[v_m^{\text{det}}]\}] & \text{(C.15)}\\
&= \sum_{c,d=1}^{k} \sum_{a,b=1}^{p} A_a A_b |T_{lc}(\omega_a)| \frac{\partial f_c}{\partial u_a} |T_{md}(\omega_b)| \frac{\partial f_d}{\partial u_b} \\
&\quad \times \int_{-\infty}^{\infty} \cos(\omega_a t + \phi_a + \xi_{lc}(\omega_a)) \cos(\omega_b(t+\tau) + \phi_b + \xi_{md}(\omega_b)) dt
\end{aligned}
$$

$$
\begin{aligned}
\mathcal{C}_{x_l x_m}^{\text{ran}}(\tau) &= \mathbf{E_t}[\{v_l^{\text{ran}}(t) - \mathbf{E_t}[v_l^{\text{ran}}]\}\{v_m^{\text{ran}}(t+\tau) - \mathbf{E_t}[v_m^{\text{ran}}]\}] & \text{(C.16)}\\
&= \sum_{c,d=1}^{k} \sum_{a,b=1}^{p} \frac{1}{2\pi} \int_{-\infty}^{+\infty} T_{lc}(\omega) \frac{\partial f_c}{\partial u_a} T_{md}(-\omega) \frac{\partial f_d}{\partial u_b} \mathcal{S}_{\delta r_a \delta r_b}(\omega) e^{i\omega\tau} d\omega
\end{aligned}
$$

$$\mathcal{C}^{\text{dem}}_{x_l x_m}(\tau) = \mathbf{E_t}[\{v_l^{\text{dem}}(t) - \mathbf{E_t}[v_l^{\text{dem}}]\}\{v_m^{\text{dem}}(t+\tau) - \mathbf{E_t}[v_m^{\text{dem}}]\}] \tag{C.17}$$

$$= \sum_{c,d=1}^{k} \frac{1}{2\pi} \int_{-\infty}^{+\infty} T_{lc}(\omega) q_c^{1/2} T_{md}(-\omega) q_d^{1/2} e^{i\omega\tau} d\omega \, .$$

Note that all expressions are to be evaluated at $(\mathbf{x}_1, \mathbf{u}_0)$. The term $\mathcal{S}_{\delta r_a \delta r_b}(\omega) = \int_{-\infty}^{\infty} \mathcal{C}_{\delta r_a \delta r_b}(t) \exp(-i\omega t) dt$ in expression (C.16), known as the spectral density, is simply the Fourier transformation of $\mathcal{C}_{\delta r_a \delta r_b}(t)$ which is the *autocorrelation* of the environmental stochasticity, $\delta\mathbf{r}$. Note that in many cases cross-correlations $\mathcal{C}_{\delta r_a \delta r_b}(\tau)$ $(a \neq b)$ will be zero since fluctuations in different model parameters are likely to be independent. The above expressions (C.15)−(C.17) can often be evaluated analytically for $\tau = 0$, and also in simple cases for $\tau > 0$, (see Section 2.2). Otherwise numerical integration is required.

Appendix D: Notation

General

$n(t)$	−	population size in discrete stochastic models
$x(t)$	−	population size in continuous models
$\mu(t)$	−	death rate in immigration-death model
$\nu(t)$	−	immigration rate in immigration-death model
$p(n;t)$	−	probability of population size n at time t
$M(\theta;t)$	−	moment generating function $\mathbf{E}[\exp(\theta n)]$
$\mathbf{E}[n^j]$	−	jth moment of n, e.g. the mean is the first-order moment
$K(\theta;t)$	−	cumulant generating function $K = \ln M$
κ_j	−	jth cumulant, e.g. κ_2 is the variance.
$G(z;t)$	−	probability generating function $G(z,t) = \sum_{n=0}^{\infty} p(n;t)z^n$
Z_ν	−	mean-reverting Uhlenbeck-Ornstein process, perturbing parameter ν
b_ν	−	exponential correlation parameter for Z_ν
$\bar{Z}_\nu$	−	mean (in equilibrium) of Z_ν
$\sigma^2_{Z_\nu} = \sigma^2_\nu / 2b_\nu$	−	variance (in equilibrium) of Z_ν
$B(Z), D(Z)$	−	transformations of Z e.g. $\nu(t) = B(Z_\nu)$
$\mathcal{C}_{x_l x_m}(\tau)$	−	time-lagged auto- and cross-correlations
$\mathbf{T}(\omega)$	−	transfer function matrix

Helminth model

$n_L(t)$	−	free-living larval population
$n_A(t)$	−	adult parasite population
$n_r(t)$	−	host immunity level
$\beta(t)$	−	contact rate of infection
$\widetilde{\beta}(t)$	−	weather-driven fluctuations in contact rate
$q(t)$	−	probability of egg development
$\rho(t)$	−	death rate of free-living stage
σ	−	rate of loss of immunological memory
$\lambda(n_r)$	−	rate of egg production
$\mu(n_r)$	−	adult mortality rate
$p(n_r)$	−	probability of parasite establishment

TABLE I

Var[ν]		$\mathbf{E}[n]$	Var[n]	Cfd. Intvl.
1	Norm. approx.	5.0	5.663	$(0.34, 9.66)$
	Simulation	4.996	5.672	$(0, 10)$
5	Norm. approx.	5.0	8.246	$(-0.63, 10.63)$
	Simulation	4.999	8.329	$(0, 11.52)$
35	Norm. approx.	5.0	21.515	$(-4.09, 14.09)$
	Simulation	5.005	26.66	$(0, 18.11)$

Comparison of Normal approximation and simulation: Mean, variance and 95% confidence intervals for the immigration-death model population size with $\nu = B(Z_\nu) = Z_\nu^2$. Parameter values are $\mathbf{E}[\nu] = 5$, $\mu_0 = 1$, $b_\nu = 0.5$, and var[ν] as shown.

TABLE II

$p(0)$	$= 0.65$		q	$= 0.35$
β	$= 0.365$		ρ	$= 7$
$\mu(0)$	$= 25$		σ	$= 0.01$
$p'(r)$	$= \mu'(r) = 0$		$\lambda(r)$	$= \lambda_0 \exp(-\lambda_1 r)$
λ_1	$= 10^{-6}$		λ_0	$= 39420$

Parameter values: suggested by Roberts and Grenfell (1991); $p(0)$, q, r and λ_1 are dimensionless, whilst the remaining quantities are in units of year^{-1}.

TABLE III

Var[q]	b_q		σ_L	
		Simulation	Local lin.	Norm. approx.
10^{-7}	50	30620	31147	38380
	0.5	35640	31415	38920
10^{-6}	50	35010	31188	38480
	0.5	39950	33770	-

Comparison of Normal and linear approximations to simulation: Standard deviation σ_L in free-living population from simulations of $t = 0, ..., 5000$ years, and the equilibrium solution of the Normal and linear approximations when $q = B(Z_q) = Z_q^2$. Parameter values are as in Table II, with $\mathbf{E}[q] = 0.35$ and b_q and var[q] as shown.

TABLE IV

Var$[q]$	b_q	Measures of extinction		
		Simulation %	Local lin. $\sigma_L/\mathbf{E}\left[n_L(t)\right]$	Norm. approx. $\sigma_L/\mathbf{E}\left[n_L(t)\right]$
10^{-4}	50	0	0.4495	$-$
	0.5	54	1.702	$-$
10^{-3}	50	2	0.785	$-$
	0.5	100	5.250	1.047

Extinction: Simulation results showing the percentage of runs up to $t = 200$ years corresponding to extinction. The coefficients of variation $\sigma_L/\mathbf{E}\left[n_L(t)\right]$ calculated from the Normal and linear approximations are shown. Here $q = B(Z_q) = Z_q^2$ with the mean $\mathbf{E}[q] = 0.35$ and b_q and var$[q]$ as shown. Other parameters are as in Table II.
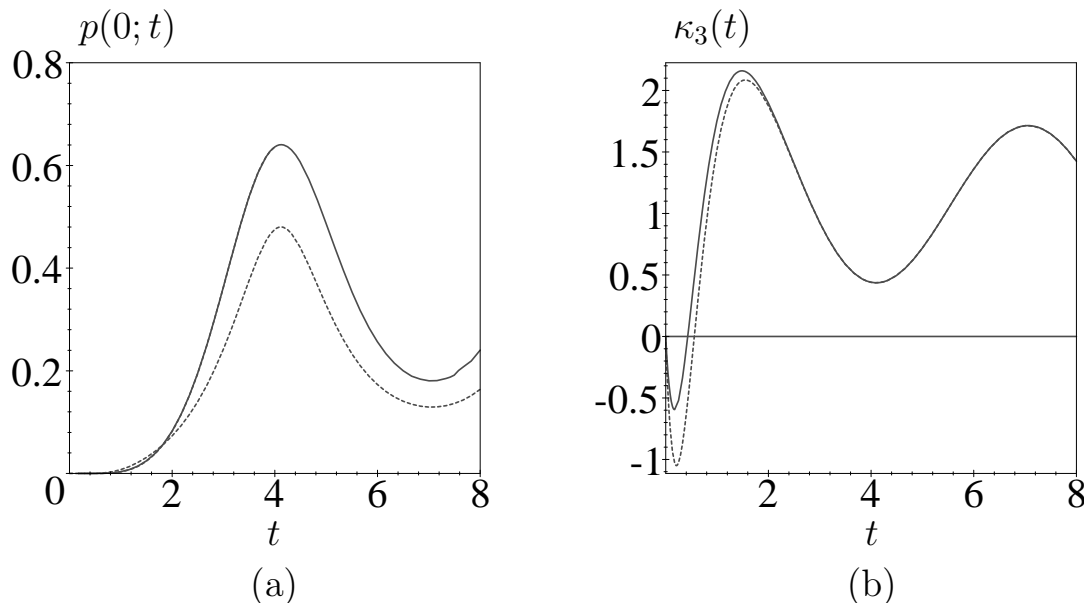
Figure 1: **Distributional approximations.** (a) $p(0;t)$ for the immigration-death process with sinusoidally varying immigration rate (solid curve) and Normal (dotted) approximation. On the scale of the figure, the binomial approximation is indistinguishable from the exact calculation. (b) The third-order cumulant κ_3, (solid) and its binomial approximation (dotted). The Normal approximation to κ_3 is zero. In both graphs $\mu = 1$, $\nu(t) = 1 + \cos(t)$ and $n_0 = 10$.
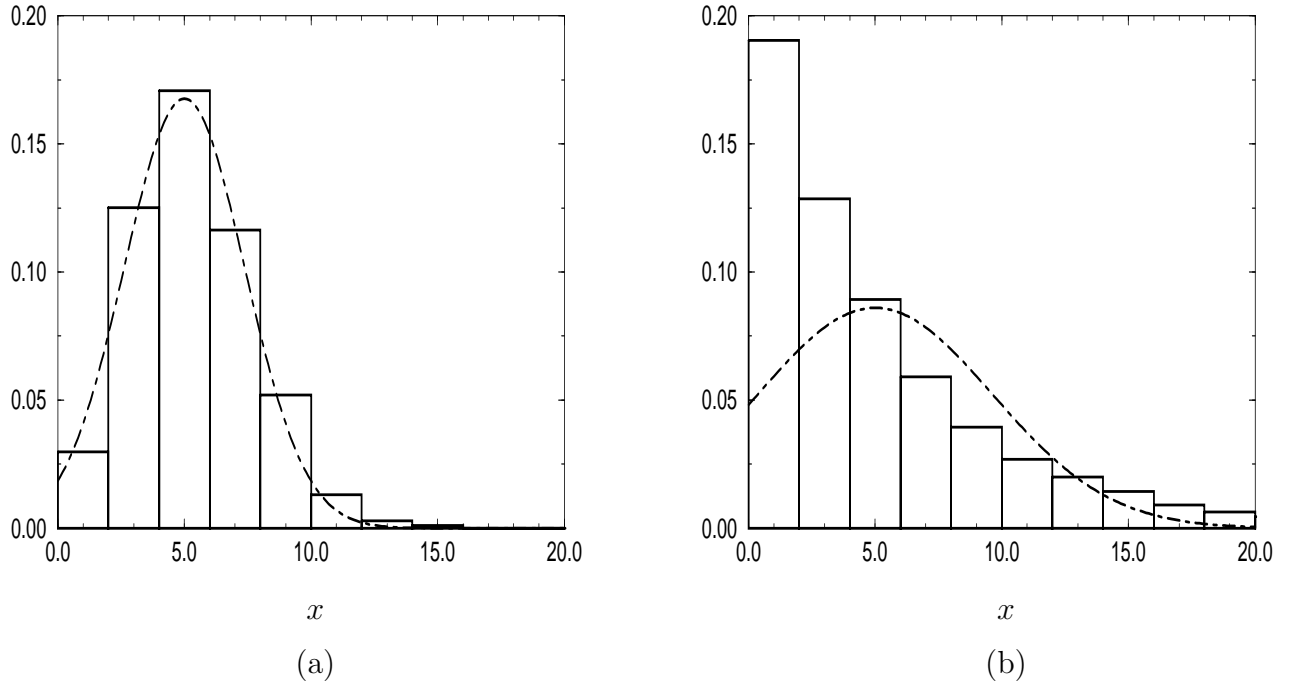
Figure 2: **Normal approximation.** Histograms of samples from repeated realizations of the immigration-death process with $\nu(t) = Z_\nu(t)^2$, $\mathbf{E}[\nu] = 5$, $\mu_0 = 1$ and $b_\nu = 0.5$. The samples are collected in the latter stages ($t = 900, ..., 1000$) of 1000 independent runs. (a) $\mathrm{var}[\nu] = 1$ and (b) $\mathrm{var}[\nu] = 35$. The dot-dashed curves show the corresponding Normal approximations to $p(n; t)$.
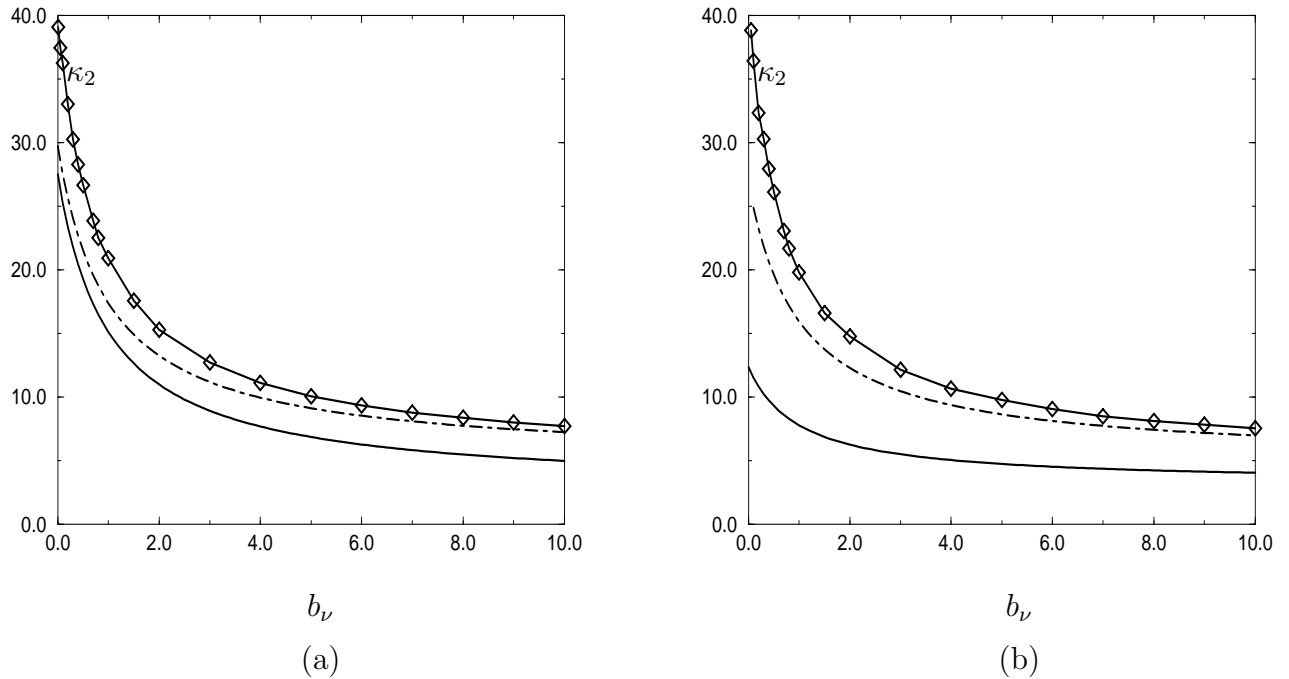

Figure 3: **Normal and Local linear approximations.** Normal (dot-dash) and local linear (solid) approximation to the population variance of the immigration-death model against b_ν with (a) $\nu = Z_\nu^2$ and (b) $\nu = \exp\{Z_\nu\}$. In each case diamonds show variances obtained from 1000 simulations for $t = 0, ..., 1000$ with $\mu = 1$ over a range of b_ν.
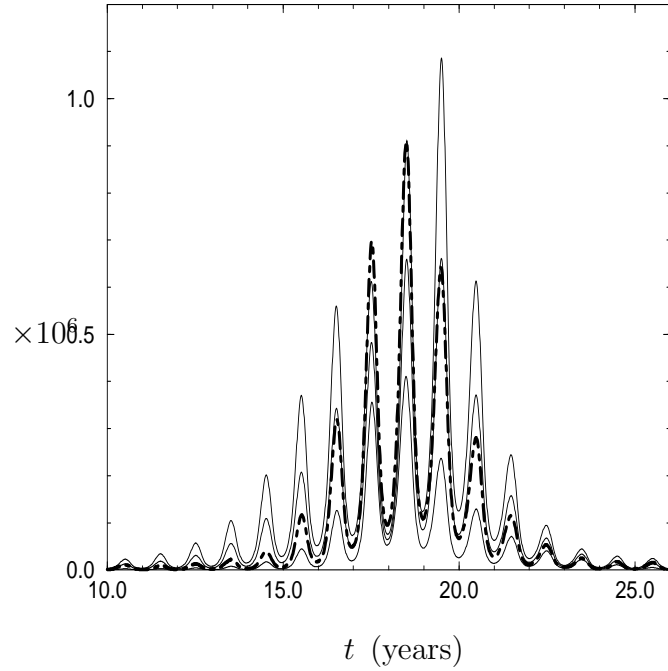
Figure 4: **Normal approximation.** Mean with ± 1 standard deviation intervals, $\mathbf{E}[n_L] \pm \sigma_L$, (solid curves) for Table II parameter values but with $q(t) = q_0 [1 + \sin(\omega t)]$. The dot-dash curve shows a simulation run. The starting conditions are the deterministic equilibrium values to the nearest integer.
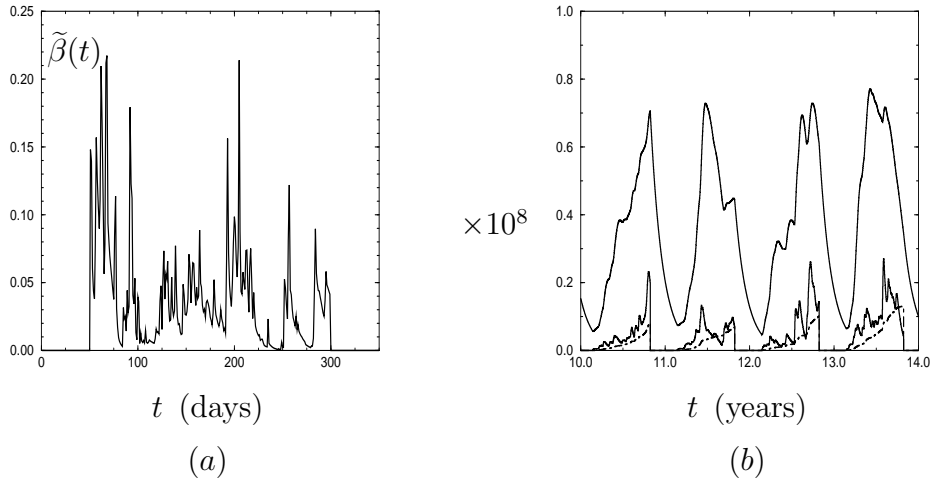

Figure 5: **Micro-climatic fluctuations.** (a) shows one year of the time series $\widetilde{\beta}(t)$ obtained from the model of Beecham (1997). The zero periods reflect the assumption that hosts are put out to pasture on the 51st day of the year and are then removed on day 300. (b) shows a standard simulation in which the contact rate is $\widetilde{\beta}(t)$ and the acquired immunity is zero when hosts are put out to pasture. Other parameter values are given in Table II. The population n_L is shown in the uppermost curve, the lower jagged curve depicts $n_A \times 100$, whilst the lower dotted curve shows $n_r \times 5$.
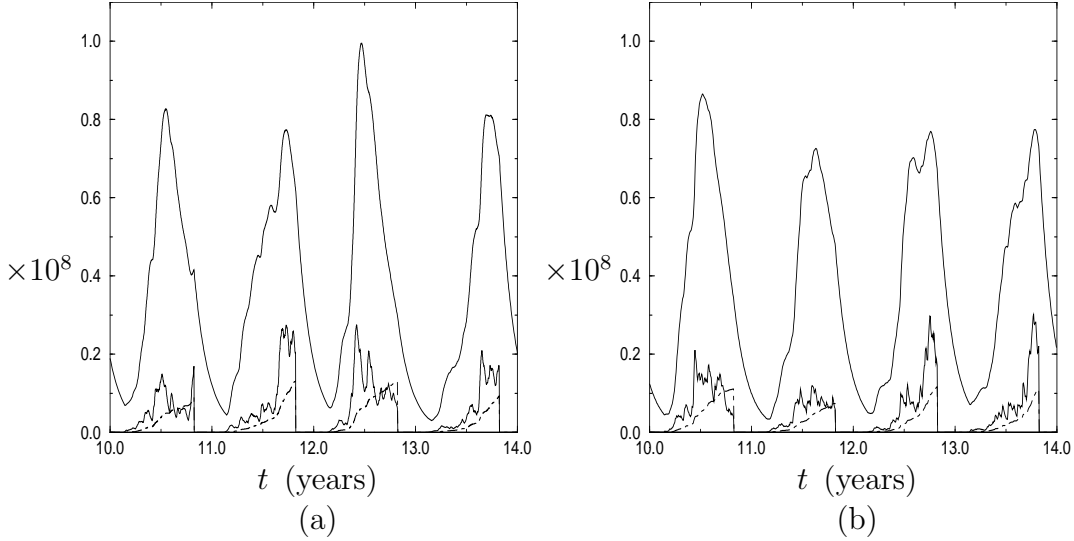
Figure 6: **Models of micro-climatic fluctuations.** Simulations using simple stochastic models of the weather-driven contact rate. In both graphs the top curve shows the free-living population $n_L(t)$, the jagged lower curve the adult population $n_A(t) \times 100$, and the dotted lower curve the immune level $n_r(t) \times 5$ from one simulation run. (a) the contact rate is modelled as the square of a third-order auto-regressive process fitted to $\widetilde{\beta}$. (b) the simulation is that resulting from the contact rate modelled by a transformed mean-reverting Uhlenbeck-Ornstein process ($\beta = Z_{\widetilde{\beta}}^2$), also fitted to $\widetilde{\beta}$. Other parameter values are given in Table II.
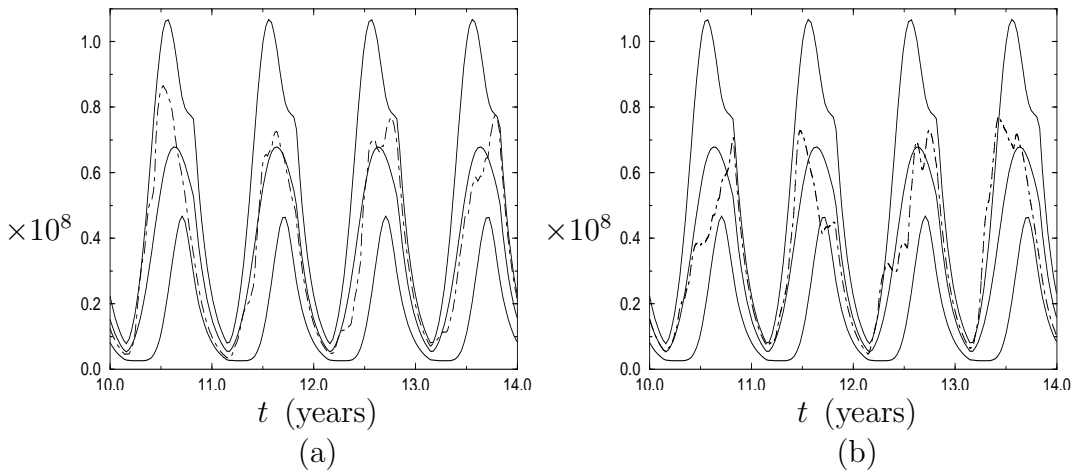

Figure 7: **Normal approximation.** Both graphs show (solid lines) the Normal approximation to $\mathbf{E}[n_L]$ and ± 2 standard deviations for the case when the contact rate $\beta = Z_{\widetilde{\beta}}^2$ is fitted to $\widetilde{\beta}$ with $b_\beta = 200$ and the other parameters values are as given in Table II. The dot-dash curve shows (a) the corresponding population fluctuations $n_L(t)$ from a simulation of the process when $\beta = Z_{\widetilde{\beta}}^2$ and (b) shows $n_L(t)$ from a simulation using the weather-driven contact rate $\widetilde{\beta}$.