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ENVIRONMENTAL VARIABILITY AND MEAN-REVERTING PROCESSES

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ABSTRACT. Environmental variability is often incorporated in a mathematical model by modifying the parameters in the model. In the present investigation, two common methods to incorporate the effects of environmental variability in stochastic differential equation models are studied. The first approach hypothesizes that the parameter satisfies a mean-reverting stochastic process. The second approach hypothesizes that the parameter is a linear function of Gaussian white noise. The two approaches are discussed and compared analytically and computationally. Properties of several mean-reverting processes are compared with respect to nonnegativity and their asymptotic stationary behavior. The effects of different environmental variability assumptions on population size and persistence time for simple population models are studied and compared. Furthermore, environmental data are examined for a gold mining stock. It is concluded that mean-reverting processes possess several advantages over linear functions of white noise in modifying parameters for environmental variability.

1. Introduction. There are numerous fundamental biological parameters, such as per capita birth or death rate, carrying capacity, infection contact rate, and recovery rate, that are constant for a given species in a non-varying environment. However, in a varying environment, these parameters also vary. In the present investigation, two approaches are examined for incorporating environmental variability into the parameters of a mathematical model for a dynamical biological system. To define the problem and to study its nature, consider the simple birth-death process modeled deterministically by

$$\frac{dy(t)}{dt} = (b(t) - d(t))y(t) \quad (1)$$

with $y(0) = y_0$ where $b(t)$ and $d(t)$ are per capita birth and death rates respectively. In a laboratory setting with no external influences, $b(t)$ and $d(t)$ are constants and (1) is an accurate model for the average population size $y(t)$. However, demographic randomness in the birth-death process is present even in a well-controlled laboratory setting. Through generalizing the deterministic model to a stochastic differential equation model, equation (1) can be modified to account for the randomness in

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births and deaths [4, 6]. Accounting for demographic randomness leads to an Itô SDE of the form

$$dy = (b(t) - d(t))y(t) dt + \sqrt{(b(t) + d(t))y(t)} dW(t) \quad (2)$$

where $W(t)$ is a standard Wiener process. In a laboratory setting with no external influences, (2) is a useful model for studying properties of the population size $y(t)$.

However, outside a laboratory setting, numerous environmental variables affect the population dynamics separately from demographic changes. One possible way to model the environmental effects would be to specifically include additional variables in the mathematical model such as weather, predator populations, competitor populations, habitat changes, and food supply. Including additional variables, however, quickly complicates the model and destroys the simple, useful nature of the original model. Consider the deterministic model (1) for the growth of a single population of size $y(t)$. In a varying environment, the per capita birth and death rates, $b(t)$ and $d(t)$, would be functions of these additional environmental variables and would have the forms $b(t, v_1, v_2, \dots, v_n)$ and $d(t, v_1, v_2, \dots, v_n)$, respectively, where v_1, v_2, \dots, v_n represent n different environmental variables. Thus, as v_1, v_2, \dots, v_n vary, the per capita birth and death rates also vary. This suggests that an approximate way to include environmental variability, without modeling the complicated behavior of many interacting environmental factors, is to allow the per capita birth and death rates to vary in a random manner. Therefore, as is often hypothesized (e.g., [3, 4, 5, 6, 8, 10, 18, 21, 23]), it is assumed that changes in the environment produce random changes in a population's per capita birth and death rates that are independent from the changes due to demographic variability. For other population models involving additional parameters, such as infection and recovery rates in an epidemic model, it is assumed that the environment would similarly affect these parameters. This hypothesis provides an approximation to the actual biological situation which leads to manageable mathematical models that give insight into the effects of environmental variability on the dynamics of a population. As a result, this hypothesis is often assumed.

For SDE models of population dynamics, there are two common approaches to modify parameters for a varying environment. The first approach assumes that the parameters satisfy mean-reverting stochastic processes, that is, each parameter satisfies a certain SDE. The second approach assumes that the parameters can be adequately modeled by linear functions of white noise. (See, for a few examples, [8, 10, 18, 19, 20, 23, 25].) The differences and similarities between these two assumptions are examined in the present investigation.

In the next section, three commonly used mean-reverting processes for modeling environmental variability in parameters are considered and compared to a linear function of white noise. In section 3, important properties of the three mean-reverting processes are summarized. Then, in sections 4 and 5, mean-reverting processes are compared with a linear function of white noise for population problems involving carrying capacity, persistence time, and in fitting environmental data. It is concluded that mean-reverting processes possess several important features that better characterize environmental variability than does a linear function of white noise. The main contribution of the present investigation arises from this conclusion, that is, mean-reverting processes offer a biologically realistic and mathematically straightforward way to treat environmental variability in SDE models.

2. Modeling environmental variability in SDEs. Two approaches to model environmental variability in the parameters $b(t)$ and $d(t)$ in (1) are considered. The first approach involves applying a mean-reverting SDE process, sometimes referred to as colored noise [11], to the parameter. The second approach is through modeling the parameter with a linear function of Gaussian white noise (WN), specifically, a linear function of the derivative of a Wiener process. A primary difference between the two approaches is that, unlike Gaussian WN, a mean-reverting process is continuously varying with time. For example, for a small time interval Δt , a mean-reverting process $X(t)$ has correlation coefficient $\rho(X(t), X(t + \Delta t)) = 1 - O(\Delta t)$ while $\rho(X(t), X(t + \Delta t)) = 0$ for Gaussian white noise. White noise processes are often used to model random disturbances with a very small correlation period. However, the environments of many biological systems, due to the large number of interacting variables, may be considered to vary in a continuous manner. Thus, mean-reverting processes may be more appropriate for modeling the parameters. Other differences between a mean-reverting process and a linear function of white noise for modeling environmental variability are examined in the following discussion.

Consider the per capita birth rate $b(t)$. The per capita death rate $d(t)$ can be treated in an analogous manner. A possible model for the birth rate in a randomly-varying environment is a linear function of Gaussian WN:

$$b(t) = \gamma + \sigma \frac{dW(t)}{dt}, \quad (3)$$

where $W(t)$ is a standard Wiener process. A conceptual problem immediately occurs in that $dW(t)/dt$ is not defined except in a generalized sense. The per capita birth rate, $b(t)$ in (3), only exists in an abstract sense and, additionally, it is difficult to directly estimate the parameters γ and σ in (3) given data for per capita birth rate. For example, by directly integrating (3), the average per capita birth rate over an interval $[0, T]$ is equal to

$$\bar{b} = \frac{1}{T} \int_0^T b(t) dt = \gamma + \sigma \frac{W(T)}{T} \sim \mathbb{N}(\gamma, \sigma^2/T). \quad (4)$$

That is, the average per capita birth rate \bar{b} over an interval of length T has a variance which goes to infinity as $T \rightarrow 0$. Indeed, successive averages of a linear function of white noise experience large random oscillations. To see this, let

$$b_i = \frac{1}{\Delta t} \int_{i\Delta t}^{(i+1)\Delta t} b(t) dt, \quad i = 1, 2, 3, \dots$$

be averages of per capita birth rate $b(t)$ over successive time intervals of length Δt . It follows that

$$b_{i+1} - b_i \sim N(0, 2\sigma^2/\Delta t)$$

and, for example, if $\sigma = 1$ and $\Delta t = 10^{-6}$, then

$$P(|b_{i+1} - b_i| > 1400) > 0.30.$$

That is, over 30% of successive average birth rates differ by more than 1400. (If instead $\Delta t = 10^{-8}$, then over 30% of successive average birth rates differ by more than 14000.) The question arises of whether it is reasonable for the average value over a time interval of a fundamental parameter, such as per capita birth rate, to become increasingly more variable as the time interval decreases.

A possible way to justify use of a linear function of Gaussian white noise is to study the effects it has on the population dynamics. Let $y(t)$ be the population size at time t . Disregarding demographic variability and assuming no deaths in the population, equation (1) and (3) imply that $y(t)$ satisfies the Itô SDE

$$dy(t) = \gamma y(t) dt + \sigma y(t) dW(t). \quad (5)$$

Using Itô's formula [9, 17], it is seen that $\log(y(t))$ satisfies the equation

$$\log(y(t)) = \log(y(0)) + (\gamma - \sigma^2/2)t + \sigma W(t)$$

and so,

$$\log(y(t)) \sim \mathbb{N}(\log(y(0)) + (\gamma - \sigma^2/2)t, \sigma^2 t).$$

That is, at any time t , the population size satisfies a log-normal distribution with $\mathbb{E}(\log(y(t))) = \log(y(0)) + (\gamma - \sigma^2/2)t$. Although the average of the logarithm of population size over an interval of length T has variance which goes to infinity as $T \rightarrow 0$, a log-normal distribution may appear reasonable for a population undergoing environmental variability. Also, the parameters γ and σ can be estimated given data on the population size with time. Unfortunately, the per capita birth rate is still undefined except in a generalized setting. An important question still remains, specifically, how can (5) be biologically justified and, thus, how can (5) be relied on for providing insight into the dynamics of a population in a randomly varying environment.

A possible way to eliminate the conceptual and practical difficulties associated with linear functions of Gaussian WN is by considering the parameters in a randomly varying environment as mean-reverting processes. In this alternate approach, the parameters $b(t)$ and $d(t)$ satisfy separate SDEs. The SDEs are structured so that the per capita rates cannot drift off to infinity, i.e., they are forced back to asymptotic mean values. These SDEs are called mean-reverting and are commonly used, for example, in financial models. As above, consider in detail the per capita birth rate. Let b_e be the asymptotic mean value of the per capita birth rate in the varying environment. When $b(t) \neq b_e$, then the probability of moving closer to b_e is greater than the probability of moving further away from b_e . In this way, unrealistic values for the per capita birth and death rates are avoided. Indeed, discrete stochastic models can be derived that lead to mean-reverting processes [4, 6]. In the following, several well-known and useful mean-reverting models are examined.

A classic mean-reverting process is the Ornstein-Uhlenbeck (OU) process which, for the per capita birth-rate, has the form:

$$db(t) = \gamma_b(b_e - b(t)) dt + \sigma_b dW_2(t). \quad (6)$$

With a similar equation for $d(t)$, a stochastic differential equation system is obtained for (2) of the form

$$\begin{cases} dy(t) = (b(t)y(t) - d(t)y(t)) dt + \sqrt{(b(t)y(t) + d(t)y(t))} dW_1(t) \\ db(t) = \gamma_b(b_e - b(t)) dt + \sigma_b dW_2(t) \\ dd(t) = \gamma_d(d_e - d(t)) dt + \sigma_d dW_3(t) \end{cases} \quad (7)$$

for $(y(t), b(t), d(t)) \in [0, \infty) \times \mathbb{R}^1 \times \mathbb{R}^1$ where $W_i(t), i = 1, 2, 3$ are independent standard Wiener processes. (Three Wiener processes are necessary to model the

demographic and environment changes.) System (7) represents a stochastic model of a single population experiencing both demographic and environmental variability.

The stochastic differential equation (6) for $b(t)$ can be solved exactly to yield

$$b(t) = b_e + \exp(-\gamma_b t) \left(-b_e + b(0) + \int_0^t \sigma_b \exp(\gamma_b s) dW_2(s) \right). \quad (8)$$

Indeed, equation (8) implies that

$$b(t) \sim \mathbb{N}(b_e + \exp(-\gamma_b t)(-b_e + b(0)), \frac{\sigma_b^2}{2\gamma_b}(1 - \exp(-2\gamma_b t)))$$

and, asymptotically with time t , it follows that the per capita birth rate $b(t)$ is normally distributed with mean b_e and variance $\sigma_b^2/(2\gamma_b)$. Thus, it is inherently assumed in this stochastic model that random variations in the environment cause the per capita birth rate to vary about an asymptotic mean value b_e for any large time t . An analogous result applies to the per capita death rate.

Now consider the mean birth rate over an interval of size T assuming, for convenience, that $b(0) = b_e$. Then, integrating (8) and simplifying,

$$\bar{b} = \frac{1}{T} \int_0^T b(t) dt = b_e + \frac{1}{T} \int_0^T \frac{\sigma_b}{\gamma_b} (1 - \exp(\gamma_b(s - T))) dW_2(s). \quad (9)$$

It follows that $\mathbb{E}(\bar{b}) = b_e$ and for small T ,

$$\text{Var}(\bar{b}) = \frac{\sigma_b^2 T}{3} + O(T^2).$$

Thus, as $T \rightarrow 0$, $\bar{b} \rightarrow b_e$ with zero variance. Unlike when the per capita birth rate is a linear function of white noise in (4), the variance goes to 0 rather than ∞ as $T \rightarrow 0$.

A disadvantage of the Ornstein-Uhlenbeck process is that it is possible for $b(t)$ to have negative values. To avoid negative values, financial mathematicians often use a Cox-Ingersoll-Ross (CIR) [1, 2] mean-reverting SDE model which, for birth rate $b(t)$, has the form

$$db(t) = \gamma_b(b_e - b(t)) dt + \sigma_b(b(t))^{1/2} dW_2(t) \quad (10)$$

with $b(0) = b_0 > 0$. Applying Itô's formula, the mean and mean square in the birth rate for this model satisfy the ordinary differential equations

$$\frac{d\mathbb{E}(b(t))}{dt} = \gamma_b(b_e - \mathbb{E}(b(t)))$$

$$\frac{d\mathbb{E}(b^2(t))}{dt} = (2\gamma_b b_e + \sigma_b^2)\mathbb{E}(b(t)) - 2\gamma_b \mathbb{E}(b^2(t)).$$

Solving this ODE system gives $\mathbb{E}(b(t)) = b_e + (b_0 - b_e)e^{-\gamma_b t}$ and

$$\text{Var}(b(t)) = \frac{\sigma_b^2 b_e}{2\gamma_b} + \frac{\sigma_b^2(b_0 - b_e)}{\gamma_b} e^{-\gamma_b t} + \left(\frac{\sigma_b^2 b_e}{2\gamma_b} - \frac{\sigma_b^2 b_0}{\gamma_b} \right) e^{-2\gamma_b t}.$$

For the CIR model, as $t \rightarrow \infty$, then $\mathbb{E}(b(t)) \rightarrow b_e$ and $\text{Var}(b(t)) \rightarrow \frac{\sigma_b^2 b_e}{2\gamma_b}$. An important feature of the CIR model is that the birth rate, $b(t)$, is nonnegative with probability one for any $t \geq 0$. The probability density of the stochastic differential equation (10) satisfies [12, 13]:

$$p(t, b) = c \left(\frac{v}{u} \right)^{q/2} e^{-u-v} I_q(2\sqrt{uv}),$$

where

$$c = \frac{2\gamma_b}{\sigma_b^2(1 - e^{-\gamma_b t})}, \quad u = cb_0 e^{-\gamma_b t}, \quad v = cb, \quad q = \frac{2\gamma_b b_e}{\sigma_b^2} - 1,$$

and $I_q(z)$ is the modified Bessel function of order q . That is,

$$I_q(z) = \left(\frac{z}{2}\right)^q \sum_{k=0}^{\infty} \frac{\left(\frac{z^2}{4}\right)^k}{k! \Gamma(q + k + 1)}$$

where Γ is the gamma function. Using the identity

$$\int_0^{\infty} e^{-cb} b^{\alpha} db = \Gamma(\alpha + 1)/c^{\alpha+1},$$

it follows that $\int_0^{\infty} p(t, b) db = 1$ for any $t > 0$. That is, $b(t) \geq 0$ with probability one for any time $t \geq 0$ for the CIR SDE model.

The OU and CIR models in equations (6) and (10), respectively, are important special cases of a general family of mean-reverting processes of the form

$$db(t) = \gamma_b(b_e - b(t)) dt + \sigma_b(b(t))^{\nu} dW_2(t). \quad (11)$$

where $0 \leq \nu \leq 1$. It is known, for example, that SDE (11) has nonnegative solutions when $1/2 \leq \nu \leq 1$ [1, 2]. A third mean-reverting process, in addition to the OU and the CIR models, that is commonly applied but is not a member of SDE family (11) is a log-normal process. For the per capita birth rate, $\log(b(t))$ satisfies the mean-reverting SDE

$$d\log(b(t)) = \gamma_b(\log(b_e) - \log(b(t))) dt + \sigma_b dW_2(t). \quad (12)$$

This model is referred to as the Black-Karasinski (BK) model in mathematical finance [7]. Letting $y(t) = \log(b(t))$ and $y_e = \log(b_e)$, then $y(t)$ satisfies the OU SDE

$$dy(t) = \gamma_b(y_e - y(t)) dt + \sigma_b dW_2(t). \quad (13)$$

Assuming that $y(0) = y_e$ and as equations (6) and (13) are identical in form, it follows from the argument for equation (6) that

$$y(t) \sim \mathbb{N}(\log(b_e), \frac{\sigma_b^2}{2\gamma_b}(1 - \exp(-2\gamma_b t))).$$

Since $b(t) = \exp(y(t))$, then $b(t)$ is log-normal for all t . For large t , the probability density of $b(t)$ approaches a stationary log-normal density with mean and variance equal, respectively, to $b_e \exp(\sigma_b^2/4\gamma_b)$ and $b_e^2 (\exp(\sigma_b^2/\gamma_b) - \exp(\sigma_b^2/(2\gamma_b)))$. (Note that if $z \sim \mathbb{N}(0, s^2)$, then $\mathbb{E}(\exp(z)) = \exp(s^2/2)$ and $\text{Var}(\exp(z)) = \exp(2s^2) - \exp(s^2)$.)

3. Properties of several mean-reverting processes. Some additional properties of the three mean-reverting processes, discussed in the previous section, are presented in this section. Denoting the three random variables for these processes as $r_i(t)$, $i = 1, 2, 3$, they satisfy the Itô SDEs:

$$dr_1(t) = \gamma_1(r_{e,1} - r_1(t)) dt + \sigma_1 dW_1(t) \quad (14)$$

$$dr_2(t) = \gamma_2(r_{e,2} - r_2(t)) dt + \sigma_2(r_2(t))^{1/2} dW_2(t) \quad (15)$$

$$d\log(r_3(t)) = \gamma_3(\log(r_{e,3}) - \log(r_3(t))) dt + \sigma_3 dW_3(t) \quad (16)$$

where $r_i(0) = r_{i,0}$, $W_i(t)$ are standard Wiener processes, and γ_i and σ_i are constants for $i = 1, 2, 3$. SDEs (14), (15), and (16) are the OU, CIR, and log-normal

BK models, respectively. Several useful properties of these three mean-reverting processes are listed in Table 1. They possess several relevant properties for a biological parameter including continuity, reversion to a mean value, and approach to an asymptotic stationary distribution. In addition, the CIR and BK models are nonnegative. The stationary probability densities for these three SDEs can be derived from the formulas presented in Section 2 and are given, respectively, by

$$p_1(r_1) = \sqrt{\frac{\gamma_1}{\pi\sigma_1^2}} \exp\left(\frac{-\gamma_1(r_{e,1} - r_1)^2}{\sigma_1^2}\right),$$

$$p_2(r_2) = \frac{r_2^{\left(\frac{2\gamma_2 r_{e,2}}{\sigma_2^2} - 1\right)}}{\Gamma\left(\frac{2\gamma_2 r_{e,2}}{\sigma_2^2}\right) \left(\frac{\sigma_2^2}{{2\gamma_2}}\right)^{\left(\frac{2\gamma_2 r_{e,2}}{\sigma_2^2}\right)}} \exp\left(\frac{-2\gamma_2 r_2}{\sigma_2^2}\right),$$

and

$$p_3(r_3) = \sqrt{\frac{\gamma_3}{r_3^2 \pi \sigma_3^2}} \exp\left(\frac{-\gamma_3(\log(r_{e,3}) - \log(r_3))^2}{\sigma_3^2}\right).$$

For example, for the CIR model (15) noting from Section 2 that $p(t, b)$ can be written as

$$p(t, b) = ce^{-u/v} v^q e^{-u-v} \sum_{k=0}^{\infty} \frac{(uv)^k}{k! \Gamma(q + k + 1)},$$

it follows as $t \rightarrow \infty$, then $u \rightarrow 0$, $c \rightarrow \hat{c} = \frac{2\gamma_b}{\sigma_b^2}$, $v \rightarrow \hat{v} = \hat{c}b$, and

$$p(t, b) \rightarrow \frac{\hat{c}\hat{v}^q e^{-\hat{v}}}{\Gamma(q + 1)}$$

which is the desired result.

The stationary probability densities are illustrated in Figure 1 each with a mean of 10 and a variance of 12.5. Notice that the BK and CIR densities are both non-negative.

The sample paths of these mean-reverting processes are influenced by the stationary means and variances as well as the correlation coefficient $\rho(X(t), X(t + \Delta t))$ which is a measure of the dependence of the sample path on the previous position. Assuming at time t that $X(t)$ satisfies the asymptotic probability density and estimating $X(t + \Delta t)$ for small Δt using the Euler-Maruyama [14] approximation, the correlation coefficient satisfies $1 - \rho(X(t), X(t + \Delta t)) \propto \gamma_i \Delta t$. This implies that the dependence of the sample path on the previous position decreases as γ_i increases. This property is illustrated in Figure 2 for the CIR process (15) where the stationary mean and variance are kept constant at 100 and 10, respectively, but γ_2 increases from 5 to 20 to 80 in the three plots. (In the calculations, $r_{e,2}$ is fixed and σ_2 changes with γ_2 to keep the stationary variance constant.) This figure indicates the flexibility of mean-reverting processes for modeling the variability in parameters as a result of a varying environment.

4. Comparison between environmental variability hypotheses. In this section, it is investigated how the population dynamics are affected by the assumption made about the parameters in a varying environment. Specifically, the dynamics of three simple population models are compared where, in these models, the parameters are assumed to be either linear functions of white noise or mean-reverting

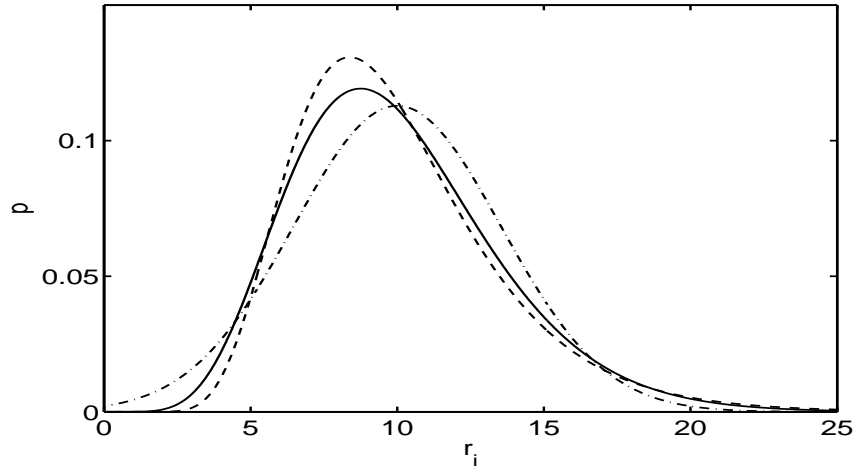


FIGURE 1. Stationary probability densities for mean-reverting OU (dashdot), CIR (solid), and BK (dashed) when mean and variance are 10 and 12.5, respectively

Property	SDE (14)	SDE (15)	SDE (16)
Solution Continuous wpl	yes	yes	yes
Solution Nonnegative wpl	no	yes	yes
Asymptotic Stationary Dens.	Normal	Gamma	Log-normal
Asymptotic Mean	$r_{e,1}$	$r_{e,2}$	$r_{e,3} \exp(\sigma_3^2/4\gamma_3)$
Asymptotic Variance	$\sigma_1^2/(2\gamma_1)$	$\sigma_2^2 r_{e,2}/(2\gamma_2)$	$r_{e,3}^2 \exp(\sigma_3^2/\gamma_3)$ $-r_{e,3}^2 \exp(\sigma_3^2/(2\gamma_3))$

TABLE 1. Several Properties of the Mean-Reverting SDEs (14), (15), (16)

processes. The first model is a simple death model where the variance in population size is compared for the two assumptions on environmental variability. In the second model, carrying capacity varies due to environmental variability and population size is compared. In the third model, growth rate varies due to environmental variability and persistence time is compared. These examples illustrate that the population dynamics can differ significantly for WN or mean-reverting hypotheses.

4.1. Death process. The simplest example, which illustrates a difference in the population dynamics between the two hypotheses, is the elementary death process

$$dy(t) = -d(t)y(t) dt, \quad y(0) = y_0, \quad (17)$$

where per capita death rate $d(t)$ is randomly varying due to the environment. Assuming that $d(t)$ is a linear function of white noise, specifically,

$$d(t) = d_e + \sigma \frac{dW(t)}{dt}, \quad d(0) = d_e, \quad (18)$$

then population size $y(t)$ satisfies the SDE

$$dy(t) = -d_e y(t) dt - \sigma y(t) dW(t), \quad y(0) = y_0. \quad (19)$$

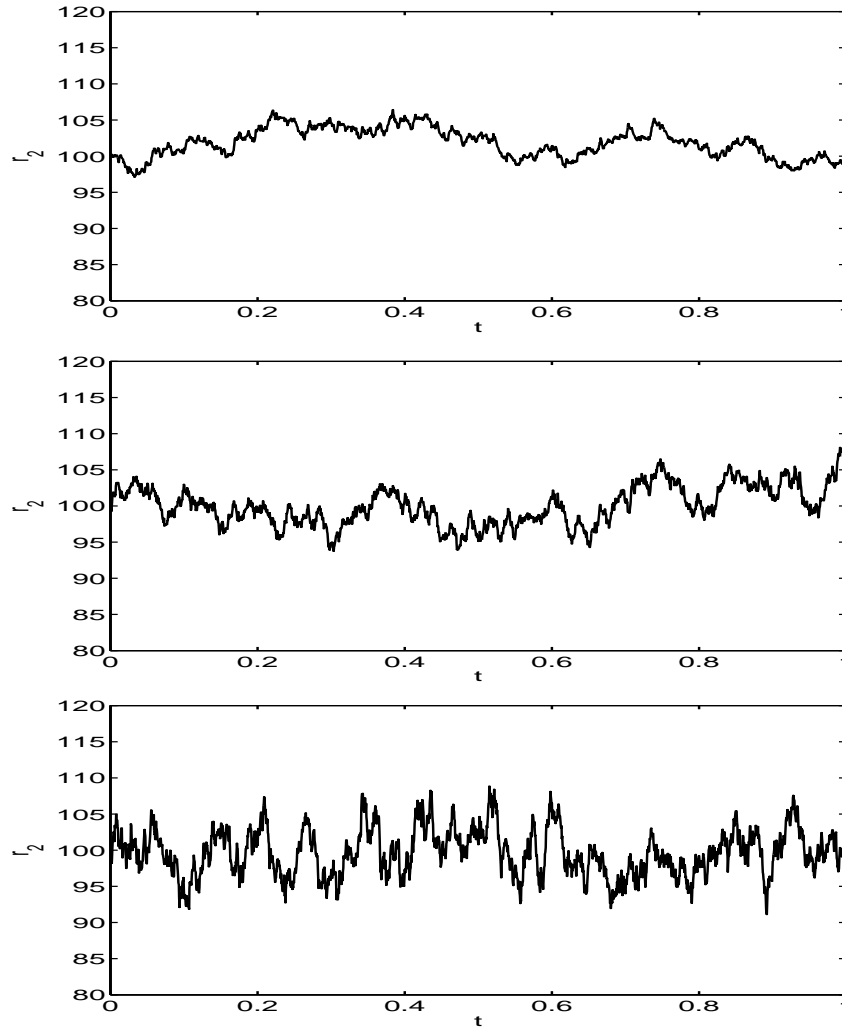


FIGURE 2. One sample path of the CIR process where the stationary mean and variance are 100 and 10, respectively, but $\gamma_2 = 5, 20, 80$ in top to bottom plots

For (19), the mean and variance in population size exactly satisfy

$$\mathbb{E}(y(t)) = y_0 \exp(-d_e t) \quad \text{and} \quad \text{Var}(y(t)) = y_0^2 \exp(-2d_e t) (\exp(\sigma^2 t) - 1). \quad (20)$$

Next, a CIR mean-reverting process for $d(t)$ is assumed of the form

$$dd(t) = \gamma(d_e - d(t)) dt + \sigma(d(t))^{1/2} dW(t), \quad d(0) = d_0 > 0. \quad (21)$$

For model (17), with $d(t)$ satisfying the mean-reverting SDE (21), population size $y(t)$ satisfies $y(t) = y_0 \exp(-\int_0^t d(s) ds)$. For this model, the mean $\mathbb{E}(y(t))$ and variance $\text{Var}(y(t))$ are bounded for all time t as $d(t) \geq 0$ with probability one.

To illustrate a difference in the population dynamics between the two hypotheses with respect to the form chosen for $d(t)$, notice that if the mean time-averaged death rate d_e is less than $\sigma^2/2$, then the variance $\text{Var}(y(t)) \rightarrow \infty$ as $t \rightarrow \infty$ for the linear function of white noise while the variance is bounded for the mean reverting process.

4.2. Population carrying capacity. In this subsection, the simple population model

$$dy(t) = a(N(t) - y(t)) dt \quad (22)$$

is studied where $N(t)$ is considered the carrying capacity of the population. It is assumed in this subsection that $N(t)$ is randomly varying due to the environment and parameter a is constant. To see how environmental variability affects the dynamics, demographic variability is not treated. First, it is assumed that $N(t)$ satisfies a linear function of Gaussian WN:

$$N(t) = \alpha + \beta \frac{dW(t)}{dt} \quad (23)$$

where α and β are constants and $W(t)$ is a standard Wiener process. Substituting equation (23) directly into equation (22) results in the Itô SDE for population size $y(t)$ of the form

$$dy(t) = a(\alpha - y(t)) dt + a\beta dW(t). \quad (24)$$

Solving (24) yields

$$y(t) = y_0 \exp(-at) + \alpha(1 - \exp(-at)) + \exp(-at) \int_0^t a\beta \exp(a\tau) dW(\tau). \quad (25)$$

For large t , the solution approaches

$$y(t) = \alpha + \exp(-at) \int_0^t a\beta \exp(a\tau) dW(\tau) \quad (26)$$

and it follows that

$$\mathbb{E}(y(t)) = \alpha \quad \text{and} \quad \text{Var}(y(t)) = \frac{a\beta^2}{2}. \quad (27)$$

The asymptotic stationary distribution for (24) is therefore normally distributed with mean α and variance $\frac{a\beta^2}{2}$, i.e., $\mathbb{N}(\alpha, a\beta^2/2)$.

Second, it is assumed for the same population problem (22) that $N(t)$ satisfies an OU mean-reverting process. (The OU mean-reverting process is considered here but computations indicate that a CIR or BK mean-reverting process gives similar results.) In this case, the population model with environmental variability is the SDE system

$$\begin{cases} dy(t) = a(N(t) - y(t)) dt \\ dN(t) = r_1(\alpha - N(t)) dt + r_2 dW(t), \end{cases} \quad (28)$$

where $N(0) = \alpha$, $y(0) = y_0$, and a , α , r_1 , and r_2 are constants. System (28) is readily solved for $N(t)$ and $y(t)$ to obtain

$$\begin{aligned} y(t) &= y_0 \exp(-at) + \alpha(1 - \exp(-at)) \\ &+ \frac{ar_2}{a - r_1} \int_0^t (\exp(r_1(\tau - t)) - \exp(a(\tau - t))) dW(\tau) \end{aligned}$$

and

$$N(t) = \alpha + \exp(-r_1 t) \int_0^t r_2 \exp(r_1 \tau) dW(\tau).$$

As t increases, $y(t)$ approaches

$$y(t) = \alpha + \frac{ar_2}{a - r_1} \int_0^t (\exp(r_1(\tau - t)) - \exp(a(\tau - t))) dW(\tau),$$

and for large t ,

$$\mathbb{E}(y(t)) = \alpha \quad \text{and} \quad \text{Var}(y(t)) = \frac{ar_2^2}{2r_1(a + r_1)}. \quad (29)$$

Also, for large t ,

$$\mathbb{E}(N(t)) = \alpha \quad \text{and} \quad \text{Var}(N(t)) = \frac{r_2^2}{2r_1}. \quad (30)$$

The asymptotic stationary distribution for population size $y(t)$ satisfying (28) is normally distributed with mean α and variance $\frac{ar_2^2}{2r_1(a + r_1)}$.

The two different hypotheses about how $N(t)$ randomly varies, either as an OU or a WN process, makes surprisingly little difference in the dynamics of the population size. Both models for environmental variability in $N(t)$ give a stochastic differential equation system for $y(t)$ where $y(t)$ is continuous with mean and variance approaching constant values as t increases. That is, normal stationary distributions are asymptotically approached with time t under either hypothesis on the variability in $N(t)$.

There are some very important differences, though, between the two hypotheses. The first difference is in the interpretation of the parameter a in model (22). In particular, the variances of the two hypotheses are much different with respect to parameter a . As a increases, the variance of $y(t)$ for any time t increases without bound in the WN model while in the OU model, the variance approaches a constant value as a increases. In other words, how parameter a is viewed in (22) is much different for the two hypotheses.

Secondly, suppose now that both a and $N(t)$ are varying in the environment. Then, it is impossible to model both a and N using linear functions of white noise. If a and N are similarly treated with linear functions of white noise, the equation for $y(t)$ would have undefined squared terms of white noise. However, the mean-reverting models have no such restriction and a can be readily modeled in the same manner as $N(t)$, specifically, using a separate SDE for parameter a .

4.3. Population growth rate and persistence time. In this subsection, a simple persistence time problem is examined where the population size $y(t)$ satisfies

$$dy(t) = r(t)y(t) dt \quad (31)$$

with $y(0) = y_0$ and where $r(t)$ is the per capita population growth rate. Per capita population growth rate is a fundamental biological parameter which depends on the species and the environment. In a randomly varying environment, $r(t)$ varies with time t and experiences random changes from the environment. As in the previous subsection, to study how environmental variability affects the dynamics, demographic variability is not considered. The persistence time, defined as the time until the population size decreases below unity, is studied. Two forms for the variability in $r(t)$ are hypothesized. First, a linear function of WN is assumed where $r(t)$ has the form

$$r(t) = \alpha + \beta \frac{dW(t)}{dt} \quad (32)$$

and where $W(t)$ is a standard Wiener process with constants $\alpha < 0$ and $\beta > 0$ and so, $y(t)$ satisfies the Itô SDE

$$dy(t) = \alpha y(t) dt + \beta y(t) dW(t). \quad (33)$$

Second, an OU mean-reverting Itô SDE is assumed for $r(t)$. Specifically, $r(t)$ and $y(t)$ satisfy

$$\begin{cases} dr(t) = \gamma(r_e - r(t)) dt + \beta dW(t), \\ dy(t) = r(t)y(t) dt, \end{cases} \quad (34)$$

with $r(0) = r_e$ where $W(t)$ is a standard Wiener process and $\gamma > 0$, $r_e < 0$, and $\beta > 0$ are constants. The two models for $r(t)$ differ in that the mean-reverting model (34) is continuous in time t with probability one. However, the two models for $r(t)$ have several similar features. For example, letting $\bar{r} = \frac{1}{T} \int_0^T r(s) ds$ be the time-averaged growth rate, then

$$\mathbb{E}(\bar{r}) = \alpha \quad \text{and} \quad \text{Var}(\bar{r}) = \beta^2/T$$

for (32) while

$$\mathbb{E}(\bar{r}) = r_e \quad \text{and} \quad \text{Var}(\bar{r}) = \frac{\beta^2}{T\gamma^2} + \frac{\beta^2}{2T^2\gamma^3} [-4(1 - \exp(-\gamma T)) + (1 - \exp(-2\gamma T))]$$

for (34). Indeed, the mean time-averaged growth rate $\mathbb{E}(\bar{r})$ is constant and $\text{Var}(\bar{r})$ decreases to zero as T increases for either the OU or WN hypothesis.

The mean persistence time is examined for these two models. Let $T(z)$ be the persistence time and $u_1(z) = \mathbb{E}(T(z))$ be the mean persistence time where the population's initial size is z . For the WN model, where population size $y(t)$ satisfies equation (33), the mean persistence time satisfies the boundary-value problem [3, 5]:

$$-1 = \alpha z \frac{du_1(z)}{dz} + \frac{1}{2} \beta^2 z^2 \frac{d^2 u_1(z)}{dz^2} \quad (35)$$

with $u_1(1)=0$ and $u_1'(\infty) = 0$. Solving the differential equation gives

$$\mathbb{E}(T(y_0)) = \frac{\log(y_0)}{-\alpha + \frac{1}{2}\beta^2} \quad (36)$$

which is finite for $\alpha < 0$.

The second problem (34) is more difficult to analyze for persistence time. However, it can be simplified by letting $z(t) = \int_0^t r(s) ds$. Then,

$$z(t) \sim \mathbb{N} \left(r_e t, \frac{\beta^2}{\gamma^2} \left(t - \frac{2}{\gamma} (1 - \exp(-\gamma t)) + \frac{1}{2\gamma} (1 - \exp(-2\gamma t)) \right) \right)$$

and $z(t)$ satisfies the Itô SDE

$$dz(t) = r_e dt + \alpha^{1/2}(t) dW(t) \quad \text{with} \quad z(0) = 0 \quad (37)$$

where $\alpha(t) = \frac{\beta^2}{\gamma^2} (1 - \exp(-\gamma t))^2$. As exit occurs when population size $y(t)$ reaches unity, or $y_0 \exp(\int_0^t r(s) ds) = 1$, then exit occurs at the identical time when $z(t) = -\log(y_0)$. Thus, an equivalent problem for the persistence time for the SDE system (34) when $y(0) = y_0$ and exit occurs at $y(t) = 1$ is to study the persistence time for the scalar SDE (37) when $z(0) = 0$ and exit occurs at $z(t) = -\log(y_0)$.

Persistence-time problem (37) is a diffusion process with drift for one absorbing boundary. For example, with zero drift, i.e. $r_e = 0$, the mean persistence time

is infinite. Also, for example, with $\alpha(t)$ equal to a constant, the mean persistence time is exactly equal to $-\log(y_0)/r_e$. For problem (37), it is useful to consider the reliability function $R(x, t)$ which is equal to the probability that the exit time is greater than t assuming that $z(0) = x$. The mean persistence time is equal to $\int_0^\infty R(x, t) dt$ and the reliability function $R(x, t)$ satisfies the equation

$$\frac{\partial R}{\partial t} = r_e \frac{\partial R}{\partial x} + \frac{1}{2} \alpha(t) \frac{\partial^2 R}{\partial x^2} \quad (38)$$

where $R(x, 0) = 1$ for $x > -\log(y_0)$ and $R(-\log(y_0), t) = 0$. By examining $R(x, t)$, a lower bound on the mean persistence time can be shown to be proportional to $-\log(y_0)/r_e$. (Another way to estimate a lower bound is by considering the mean persistence time for a problem with two absorbing boundaries, for example, at $-\log(y_0)$ and $-1/r_e$.) In particular, as $r_e \rightarrow 0$ and a pure diffusion process is approached, the mean persistence time for (37) goes to infinity. Correspondingly, the mean persistence time for (34) goes to infinity as $r_e \rightarrow 0$.

Summarizing, it is observed that the growth rate models OU and WN give different interpretations with respect to how the parameters influence the mean persistence time. Let $\mathbb{E}(\bar{r})$ equal the average growth rate over a large time interval T . Then, as noted earlier,

$$\mathbb{E}(\bar{r}) = \alpha \text{ for WN and } \mathbb{E}(\bar{r}) = r_e \text{ for OU.}$$

For WN, the mean persistence time goes to a constant value, $2\log(y_0)/\beta^2$, as $\mathbb{E}(\bar{r}) \rightarrow 0$, whereas for OU, the mean persistence time goes to ∞ as $\mathbb{E}(\bar{r}) \rightarrow 0$. The interpretation of mean persistence is different for the two different hypotheses, WN or OU.

5. An example of environmental variability. To test and compare the SDE models in the present investigation, data directly related to a biological problem would be useful. Unfortunately, it is very difficult to find appropriate data of sufficient quality and quantity to compare SDE models for biological populations undergoing environmental variability. However, there is a plethora of accurate financial data and this data is useful in studying how populations (companies) interact in the financial environment [16, 22, 24]. Indeed, the financial market is a highly-varying environment where companies undergo population-type processes. Several researchers have demonstrated the applicability and usefulness of modeling companies as populations undergoing competition, growth, and death [16, 22, 24]. In the present section, the OU and WN hypotheses are tested on data obtained from the financial market.

Gold mining company stock prices are considered as competitive populations in an environment where gold price acts as an important environmental variable. Consider, for example, Barrick Gold Corporation (NYSE:ABX). Barrick Gold Corporation is one of the world's largest gold mining companies with mines and development projects on four continents. The stock price of Barrick Gold Corporation is correlated strongly with gold price. Consider, for example, annual ABX stock price along with gold price over the nine-year period 2002-2010 summarized in Table 2. A simple model for Barrick Gold Corporation stock price as a function of gold price is $B \approx 1.4G^{1/2}$ where B is the gold corporation stock price. Thus, gold price acts as an environmental variable for ABX stock price and a possible stochastic model for ABX stock price $B(t)$ is the Itô SDE

$$dB(t) = \alpha(\beta G^\nu(t) - B(t)) dt + \gamma dW(t),$$

where $G(t)$ is gold price and α, β, ν and γ are constants.

Date	Gold Price G (U.S. dollars per ounce)	ABX Stock Price (U.S. dollars)	$1.4G^{1/2}$
12/31/02	347.50	24.35	26.10
12/31/03	415.20	29.31	28.53
12/31/04	437.10	29.00	29.27
12/30/05	516.60	32.41	31.82
12/29/06	636.00	35.85	35.31
12/31/07	833.30	41.78	40.41
12/31/08	881.10	44.71	41.56
12/31/09	1096.50	41.46	46.36
12/31/10	1421.60	53.12	52.79

TABLE 2. Closing gold price G and Barrick Gold Corporation (ABX) stock price on last trading day from 2002 to 2010

Consider how gold price behaves dynamically as an environmental variable. Specifically, does gold price behave as a mean-reverting stochastic process or as a linear function of white noise? Two models for gold price are studied for the London afternoon gold prices on 497 trading days in 1994 and 1995, specifically, an OU mean-reverting process and a linear function of WN. These gold prices are plotted in Figure 3. The OU mean-reverting stochastic process for gold price is

$$dG(t) = a(G_e - G(t)) dt + b dW(t). \quad (39)$$

The linear function of white-noise is

$$G(t) = a + b \frac{dW(t)}{dt}. \quad (40)$$

By integrating each equation over a time interval of one day, the equations are fit to the daily price data set. Specifically, letting $t_{i+1} - t_i = h = 1$, integrating equation (39) over $[t_i, t_{i+1}]$, and approximating the integral on the right-hand side leads to the Euler-Maruyama approximation [14, 15]:

$$G_{i+1} = G_i + ha(G_e - G_i) + b\sqrt{h}\eta_i \quad (41)$$

where η_i are normally distributed numbers with zero mean and unit variance. The gold price, G_i , for $i = 1, \dots, 497$ are the data values. The transition probability of G_{i+1} given G_i is normally distributed, i.e., $p(G_{i+1}|G_i) \sim \mathcal{N}(G_i + ha(G_e - G_i), b^2h)$. Maximum likelihood estimates of a, G_e , and b for equation (39) are then obtained by minimizing

$$L(a, G_e, b) = - \sum_{i=1}^{496} \ln(p(G_{i+1}|G_i))$$

over $a, G_e, b \in \mathbb{R}$ [4]. The maximum likelihood estimates of the parameters calculated using the data are $a = 0.080$, $G_e = 383.93$, and $b = 1.86$ for the OU mean-reverting model (39). In a similar way, integrating equation (40) over $[t_i, t_{i+1}]$, leads to

$$G_i = a + \frac{b}{\sqrt{h}} \eta_i. \quad (42)$$

In this case, $p(G_{i+1}|G_i)$ is normally distributed with mean a and variance b^2/h and the maximum likelihood estimates for a and b^2/h in equation (40) are equal to the

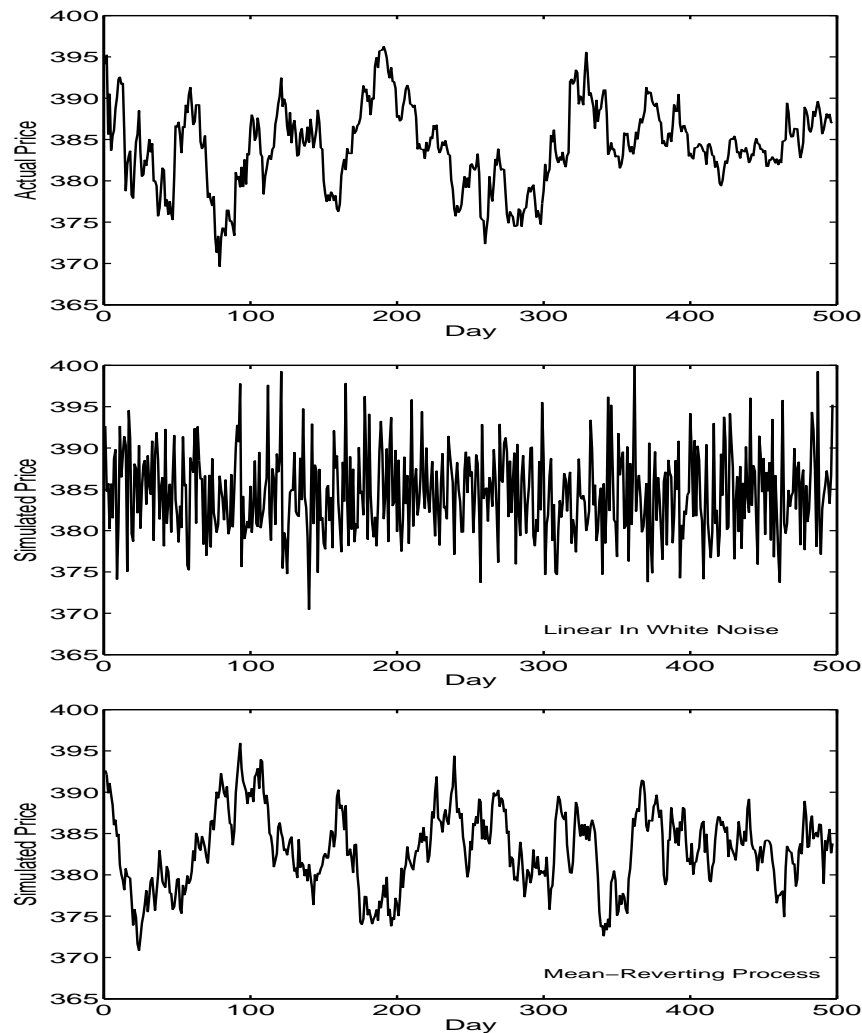


FIGURE 3. Reported gold prices for 497 days in 1994 and 1995 and simulated trajectories using a linear function of white noise and a mean-reverting process

sample mean and the sample variance. The maximum likelihood estimates of the parameters are $a = 384.11$ and $b = 4.88$ for the linear function of white noise.

A problem with the linear function of white noise (42) is the sensitivity and consistency of the time interval h to the estimation of parameters a and b . For example, if $h = 4$, over an average of four days rather than one day, then b increases from $b = 4.88$ to $b = 9.31$. A second problem with the linear function of white noise is the lack of fit with the data. One sample path of the OU and WN models, (41) and (42) respectively, were computationally simulated using the fitted parameter values. The sample paths are presented in Figure 3 along with the actual gold price data. Figure 3 clearly shows that the continuous mean-reverting process is a more realistic model for gold price than a linear function of white noise.

6. Summary and conclusions. The properties of three mean-reverting stochastic processes, defined by Itô SDEs, are summarized and compared to a linear function of Gaussian WN. The mean-reverting processes possess several important features that better characterize environmental variability in biological systems than does a linear function of white noise. Most importantly, mean-reverting processes are conceptually and biologically realistic. Other advantages of mean-reverting processes over a linear function of Gaussian WN are continuity, nonnegativity, practicality, possession of asymptotic distributions, and ease of fitting the parameters to environmental data.

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