ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 41, Number 2, 2011

STOCHASTIC EXTINCTION AND RUNAWAY GROWTH IN DISCRETE BIOLOGICAL MODELS

WILLIAM C. TROY

ABSTRACT. The consequences of global warming include predictions of 300,000 deaths per year, as well as the extinction of 100–500 species of birds per degree centigrade warming. Warming effects are also thought to play a role in runaway growth of other species, e.g., the quagga mussel invasion of Lake Mead. The mechanisms underlying runaway growth or extinction are poorly understood. We investigate these mechanisms in a discrete population equation which models the effects of environmental fluctuations of the population growth rate. The model predicts extinction when $\mathrm{E}(\ln(l))$, the geometric mean of the population growth rate, decreases below zero, and runaway growth when $\mathrm{E}(\ln(l)) > 0$. A major challenge is to estimate realizations at specific generation numbers, n, during runaway growth, or extinction, type events. Thus, we our main focus is to derive dynamic bounds which estimate realizations, at each $n \geq 1$, during the entire course of such events. These estimates are illustrated with examples. In particular, we give new insights into the dynamics of the present day ongoing Kenyan lion extinction.

1. Background and goals. At the close of the 2009 Copenhagen Climate Change conference it became increasingly clear that the nations of planet earth cannot agree on a carbon emission policy that is sufficient to stem the effects of global warming. As a result, there is a substantial probability of a 4–6 degree (Celsius) global rise in temperature by the year 2100. The consequence of such a temperature increase includes the threat of extinction of a multitude of biological species, including the human race. Already, the 2009 Global Humanitarian Forum report on the human impact of climate change and global warming estimates that "300,000 lives are lost each year due to climate change, and that nine out of ten are related to environmental degradation" [**8**]. A 2008 study [**18**] predicts that "Worldwide, every degree centigrade of warming projects a nonlinear increase of bird extinctions of 100–500 species." An August, 2009 report by the Kenya Wildlife Service states

2010 AMS *Mathematics subject classification.* Primary 34B15, 34C23, 34C11.
Keywords and phrases. Ito's lemma, extinction, geometric mean.
Received by the editors on June 4, 2010.

DOI:10.1216/RMJ-2011-41-2-615

that the country's lion population decreased from 2750 to 2000 since 2002, that this loss is partially due to climate change, and that the lions may be extinct in 20 years [**16**]. Warming effects may also be a contributing factor in the *explosive growth* of other species. For example, at the 2009 Lake Mead Symposium it was reported that "in one part of Lake Mead as many as 55,000 quagga mussels per square meter were found where none had been in January 2007. Warmer conditions, together with the right mix of food, calcium and dissolved oxygen form an ideal habitat which allows the mussels to reproduce six times per year." [**15**] The exponential increase of mussels in Lake Mead is a classic example of runaway Malthusian growth [**13**]. At this unique moment in history the global community is also facing a threat from extreme environmental fluctuations which could result from a nuclear exchange. A 2010 Scientific American article by Robock and Toon [**14**] summarizes the predictions of several mathematical climate models of the climate response to a nuclear exchange, say, between India and Pakistan. They demonstrate how a local nuclear exchange, say between India and Pakistan, could result in a 'nuclear winter' which disrupts the production of food worldwide. In turn this could cause a serious threat to the existence of the human race and other species.

In this paper we do not study extinction of a particular species. Instead, we investigate the dynamics of extinction, or runaway growth, type events in the general, yet simple, stochastic population model

$$X_{n+1} = l_{n+1} X_n, \quad X_0 > 0,\ i \geq 0, \tag{1.1}$$

where X_n and n are dimensionless variables representing a population and its generation number, respectively. We assume that the growth rate constants l_{n+1} are positive, independent, identically distributed random variables, with common pdf $f(l)$, and that

$$0 < \mathrm{E}(l) < \infty \quad \text{and} \quad \mathrm{Var}\,(l) < \infty, \tag{1.2}$$

and

$$0 < \mathrm{E}(\ln(l)) < \infty \quad \text{and} \quad \mathrm{Var}\,(\ln(l)) < \infty. \tag{1.3}$$

Thus, equation (1.1) is a model for a population in a randomly varying environment. Possible sources of environmental fluctuation include global warming effects (e.g. drought), volcanic activity, asteroid hits or the disruption of food supplies due to the effects a nuclear winter resulting from nuclear war. Realizations of (1.1) have the form

$$X_n = \left(\prod_{i=1}^{n} l_i\right) X_0. \tag{1.4}$$

Since the random variables l_i are independent, it follows from (1.2) and (1.4) that

$$\text{if } \mathrm{E}(l) > 1 \text{ then } \mathrm{E}\left(X_n\right) = \left(\mathrm{E}\left(l\right)\right)^n X_0 \to \infty \quad \text{as } n \to \infty. \tag{1.5}$$

Because of (1.5), one might expect realizations to undergo runaway growth when $\mathrm{E}(l) > 1$. To understand why this is not necessarily the case, we need to further develop the expression (1.4). It follows from (1.3) and the Law of Large Numbers that

$$\lim_{n\to\infty} \left(\prod_{i=1}^{n} l_i\right)^{1/n} = e^{\mathrm{E}(\ln(l))} \text{a.s.} \tag{1.6}$$

We refer to the number $\mathrm{E}(\ln(l))$ as the 'geometric mean' of the random variable l. Combining (1.4) and (1.6) leads, at least formally, to the approximation

$$X_n = \left(\prod_{i=1}^{n} l_i\right) X_0 \sim X_0 \exp\left(n\mathrm{E}(\ln(l))\right) \text{ a.s.} \quad \text{as } n \to \infty. \tag{1.7}$$

This predicts that realizations become unbounded when $\mathrm{E}(\ln(l)) > 0$, and that they decay to zero when $\mathrm{E}(\ln(l)) < 0$. Lewontin and Cohen [**10**] made use of the Central Limit Theorem to put these predictions on a rigorous mathematical footing, and proved the following:

$$\begin{aligned} &\text{if } e^{\mathrm{E}(\ln(l))} < 1 \text{ then } X_n \to 0 \text{ a.s.} \quad \text{as } n \to \infty, \\ &\text{if } e^{\mathrm{E}(\ln(l))} = 1 \text{ then } X_n \text{ fluctuates between large and small} \\ &\qquad\qquad\qquad \text{positive values as } n \to \infty, \\ &\text{if } e^{\mathrm{E}(\ln(l))} > 1 \text{ then } X_n \to \infty \text{ a.s.} \quad \text{as } n \to \infty. \end{aligned} \tag{1.8}$$

It follows from (1.8) that, when the geometric mean $\mathrm{E}(\ln(l))$ decreases through the critical value one, the character of realizations instantly switches from runaway growth to extinction.

Finally, we observe that the random variable l can be chosen to satisfy

$$\mathrm{E}(\ln(l)) < 0 < 1 < \mathrm{E}(l). \tag{1.9}$$

When (1.9) holds, (1.5) and (1.8) lead to the seemingly contradictory conclusion that, as $n \to \infty$, the mean $\mathrm{E}(X_n)$ becomes unbounded, yet every realization 'goes extinct' and decays to zero. This counterintuitive property is due to the uncertainty in the growth rate l, and clearly demonstrates that one needs to know *both* the mean, $\mathrm{E}(l)$, and the geometric mean $\mathrm{E}(\ln(l))$, of l in order to make meaningful conclusions about the asymptotic behavior (i.e. as $n \to \infty$) of realizations.

Goals and specific aims. When environmental fluctuations are sufficient to initiate the extinction of a population, one would like to be able to predict how long it will take until the collapse is complete. Thus, our primary goal is to answer the following modeling questions:

I. Can one predict the behavior of realizations during the entire course of an extinction or runaway growth event? In particular, can we develop dynamic estimates which predict the range of behavior of realizations, within any degree of confidence, at each generation number $n \geq 0$?

Because of the inherent uncertainty in the growth rate l, there can be a wide variation in individual realizations, even in parameter regimes where extinction, or runaway growth, is guaranteed (see Figure 1). To obtain new insights we cannot use the Central Limit Theorem approach of Lewontin and Cohen because this approach only gives limiting, asymptotic results as $n \to \infty$, and does *not* allow for rigorous estimates of realizations at small, individual n values. Instead, to answer (**I**), we need to completely analyze the probability distribution function (pdf) of the random variable $X_n = (\prod_{i=1}^{n} l_i)X_0$. For this we must choose a specific pdf for the growth rate. There is a myriad of possible choices. As a prototypical example, we assume that the constants l_i are independent, uniform random variables with

$$f(l) = \begin{cases} 1/b & \text{when } 0 < l \leq b, \\ 0 & \text{when } l \notin (0, b]. \end{cases} \tag{1.10}$$

There are two advantages of choosing the uniform random variable: (i) the values of l_i are equally probable at any point in $(0, b)$, and

(ii) the analysis of X_n is mathematically tractable. It is hoped that the results we obtain for this choice of $f(l)$ will provide a theoretical framework for future extensions to the wide range of other possible pdf's for the growth rate.

Our first observation for (1.10) is that the mean and the geometric mean of l are

$$\mathrm{E}(l) = \frac{b}{2}, \mathrm{E}(\ln(l)) = \ln\left(\frac{b}{e}\right) \quad \text{and} \quad e^{\mathrm{E}(\ln(l))} = \frac{b}{e}, \tag{1.11}$$

hence (1.7) leads to the formal prediction

$$X_n = \left(\prod_{i=1}^{n} l_i\right) X_0 \sim X_0 \left(\frac{b}{e}\right)^n \text{ a.s.} \quad \text{as } n \to \infty. \tag{1.12}$$

That is, we expect runaway growth when $b/e > 1$ and extinction if $b/e < 1$. In particular,

$$\text{if } 2 < b < e \text{ then } e^{\mathrm{E}(\ln(l))} = \frac{b}{e} < 1 < \mathrm{E}(l) = \frac{b}{2}. \tag{1.13}$$

Thus, in this range of the parameter b, we conclude that

$$\mathrm{E}(X_n) = X_0 \left(\frac{b}{2}\right)^n \to \infty \quad \text{as } n \to \infty, \tag{1.14}$$

yet each realization is predicted to 'go extinct,' i.e.,

$$X_n = X_0 \left(\frac{b}{e}\right)^n \to 0 \text{ a.s.} \quad \text{as } n \to \infty. \tag{1.15}$$

Figure 1 illustrates these properties for two different realizations of (1.4)–(1.10), each with initial condition $X_0 = 5$. When $0 \leq n \leq 14$ we let $b = 3.95$, hence the mean and geometric mean of l are

$$\mathrm{E}(l) = \frac{b}{2} = 1.825 \quad \text{and} \quad e^{\mathrm{E}(\ln(l))} = \frac{b}{e} = 1.3428 \tag{1.16}$$

and therefore,

$$\mathrm{E}(X_n) = 5\,(1.835)^n \quad \text{and} \quad X_n = 5\,(1.3428)^n\,, \quad 0 \leq n \leq 14. \tag{1.17}$$

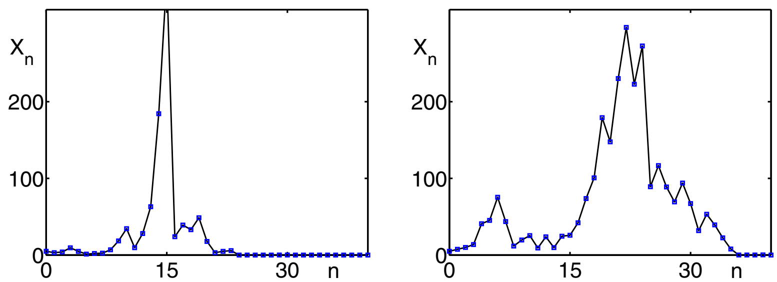

FIGURE 1. Two realizations of (1.1) when the growth rate pdf is given by (1.10). Here $X_0 = 5$, $b = 3.65 > b_{crit} = e$ and runaway growth occurs for $0 \le n \le 14$. At the critical generation number $n^* = 15$ b is reset to $b = 2.05 < b_{crit}$, and each realization goes extinct, i.e., $X_n \to 0$ as $n \to \infty$, in spite of the counterintuitive fact that the mean satisfies $\mathrm{E}(X_n) = 5(b/2)^n = 5(1.025^n) \to \infty$ as $n \to \infty$. The observation that the first realization goes extinct much earlier than the second is due to the wide variability in realizations. This wide variability is due to the uncertainty in the growth rate l.

Thus, when $0 \le n \le 14$ each realization in Figure 1 is in runaway growth mode. However, at $n = 15$ we reset b to $b = 2.05$ where the mean and geometric mean have the new values

$$\mathrm{E}(l) = \frac{b}{2} = 1.025 \quad \text{and} \quad e^{\mathrm{E}(\ln(l))} = \frac{b}{e} = 0.754 \tag{1.18}$$

Since the geometric mean is below one when $n \ge 15$, the character of realizations has switched from runaway growth to extinction, and our theoretical predictions imply that each realization goes extinct (with probability 1) as $n \to \infty$. Finally, observe that the first realization in Figure 1 goes extinct, i.e., X_n decreases below a level of sustainability, much earlier than the second. This wide variability in the rate of extinction of individual realizations is due to uncertainty in the random growth rate l. The remainder of this paper is devoted to the development of techniques to accurately predict the rate of extinction of individual realizations.

2. Theoretical predictions and examples. The predictions in (1.8) and (1.12) give criteria, in terms of the geometric mean $e^{\mathrm{E}(\ln(l))}$, for runaway growth or extinction of realizations as $n \to \infty$. However, as Figure 1 shows, when $e^{\mathrm{E}(\ln(l))} < 1$ and extinction is guaranteed, there can be a wide variability in individual realizations. A similar variability in individual realizations is observed when $e^{\mathrm{E}(\ln(l))} > 1$ and runaway growth occurs. Thus, if one wants to predict values of a realization at specific generation numbers n during an extinction or runaway growth event, then it is not sufficient to merely know the value of $e^{\mathrm{E}(\ln(l))}$. Instead, we need to fully investigate properties of the specific distribution $f(l)$ in order to predict how the uncertainty in the growth rate l affects individual realizations. Thus, our goal in this section is derive dynamic bounds which answer the following questions:

(A) Once an extinction event is initiated, say at generation number $n = 0$, can we accurately predict, within a prescribed level of confidence, the values of realizations at each $n \geq 0$?

(ii) Similarly, once a runaway growth event is initiated, say at generation number $n = 0$, can we accurately predict, within a prescribed level of confidence, the values of realizations at each $n \geq 0$?

The approach. To answer **(A)** and **(B)** we cannot use the Central Limit Theorem based method used by Lewontin and Cohen [**10**] because

(i) the Central Limit Theorem applies only 'in the limit as $n \to \infty$,' and

(ii) the Central Limit Theorem approach cannot be readily modified to give precisely estimate values of individual realizations at small generation numbers n.

To understand our approach, which is completely different from the Central Limit Theorem method, we first note that a standard criterion for proving extinction is to show that, for arbitrarily chosen $L > 0$, realizations satisfy

$$\text{Prob}\left\{X_n \leq L\right\} \longrightarrow 1 \text{ as } n \to \infty. \tag{2.1}$$

A similar criterion holds for runaway growth. To obtain the most precise estimates on realizations, our technique is to replace L in (2.1) with a suitably chosen function of the form $X_0 K^n$, where K is a constant or function of n which satisfies $0 < K < 1$, and make use of specific properties of the distribution $f(l)$ to derive a dynamic upper bound estimate of the form

$$\text{Prob}\left\{X_n \leq X_0 K^n\right\}, \quad n \geq 0. \tag{2.2}$$

The role of the function X_0K^n is to provide a measure of certainty to the uncertain values of a realization during the course of an extinction event. In Theorem 2.1 we first assume that $e^{\mathrm{E}(\ln(l))} < 1$ so that extinction must occur and derive an exact expression for the dynamic bound (2.2). Secondly, we derive an expression which dynamically estimates runaway growth type events when $e^{\mathrm{E}(\ln(l))} > 1$. Following the proof of Theorem 2.1, we give an example which demonstrates how to choose K to give optimal estimates. In a second example, we use these estimates to obtain new insights into the present day ongoing Kenyan Lion extinction

Theorem 2.1. *Let X_n denote a realization of* (1.1) *where the constant l_{i+1} is the uniform random variable whose pdf is defined by* (1.10).

(i) Extinction. *Suppose that $1 < b < e$ so that $e^{\mathrm{E}(\ln(l))} = b/e < 1$ and extinction must occur. If $K \in (0,1)$ satisfies*

$$1 < \frac{b}{K} < e, \tag{2.3}$$

then

$$\begin{aligned} \mathrm{Prob}\{X_n \leq X_0K^n\} \\ &= \frac{1}{\Gamma(n)} \int_{n\ln(b/K)}^{\infty} u^{n-1}\exp(-u)\,du \longrightarrow 1 \text{ as } n \to \infty. \end{aligned} \tag{2.4}$$

(ii) Growth. *If $M > 1$ and $b > Me$, then*

$$\begin{aligned} \mathrm{Prob}\{X_n \geq X_0M^n\} \\ &= \frac{1}{\Gamma(n)} \int_{0}^{n\ln(b/M)} u^{n-1}\exp(-u)\,du \longrightarrow 1 \text{ as } n \to \infty. \end{aligned} \tag{2.5}$$

Proof of Theorem 2.1. We first prove estimate (2.4). The details for (2.5) are similar, and are omitted. The first step is to observe that

$$\mathrm{Prob}\left\{X_n \leq X_0K^n\right\} = \mathrm{Prob}\ \left\{\ln\left(X_n\right) \leq \ln\left(X_0\right) + n\ln\left(K\right)\right\}. \tag{2.6}$$

Since $X_n = (\prod_{i=1}^n l_i)X_0$, this reduces to

$$\text{(2.7)} \qquad \text{Prob}\,\{X_n \le X_0 K^n\} = \text{Prob}\left\{ \sum_{k=1}^{n} \ln(l_k) \le n \ln(K) \right\}.$$

Let $Y_n = \sum_{k=1}^n \ln(l_k)$. Then (2.7) becomes

$$\text{(2.8)} \qquad \text{Prob}\,\{X_n \le X_0 K^n\} = \text{Prob}\,\{Y_n \le n \ln(K)\}\,.$$

It was shown in [**3**] that the cdf for Y_n is defined by

$$\text{(2.9)} \qquad \begin{gathered} \text{Prob}\,\{Y_n \le y\} = \frac{1}{\Gamma(n)} \int_{n \ln(b)-y}^{\infty} u^{n-1} \exp(-u)\, du, \\ -\infty < y \le n \ln(b), \quad n \ge 1. \end{gathered}$$

Combining (2.8) and (2.9) gives
(2.10)

$$\text{Prob}\,\{X_n \le X_0 K^n\} = \frac{1}{\Gamma(n)} \int_{n \ln(b/K)}^{\infty} u^{n-1} \exp(-u)\, du, \quad n \ge 1.$$

This completes the proof of equality in estimate (2.4). It remains to show that the right side of (2.10) approaches one as $n \to \infty$. First, note that (2.10) is equivalent to

$$\text{(2.11)} \qquad \text{Prob}\,\{X_n \le X_0 K^n\} = 1 - \frac{1}{\Gamma(n)} \int_0^{n\delta} u^{n-1} \exp(-u)\, du,$$

where $\delta = \ln(b/K) \in (0,1)$. Thus, we need to show that the integral term on the right side of (2.11) tends to zero as $n \to \infty$. For this it is convenient to prove the equivalent property
(2.12)

$$\lim_{n\to\infty} \frac{1}{\Gamma(n)} \int_0^{n\delta} u^{n-1} e^{-u}\, du = \lim_{n\to\infty} 1\Gamma(n+1) \int_0^{(n+1)\delta} u^n e^{-u}\, du = 0.$$

The substitution $u = nt$ gives

$$\text{(2.13)} \qquad \int_0^{(n+1)\delta} u^n e^{-u} du = n^{(n+1)} e^{-n} \int_0^{[(n+1)/n]\delta} e^{n(1+\ln(t)-t)}\, dt.$$

Since $0 < [(n+1)/n]\delta < 1$ when $n \gg 1$, and since the term $1+\ln(t)-t$ is increasing when $0 < t < 1$, it follows from (2.13) that

(2.14)
$$\int_0^{(n+1)\delta} u^n e^{-u} du \le n^{(n+1)} e^{-n} e^{n[1+\ln([(n+1)/n]\delta)-[(n+1)/n]\delta]} \frac{(n+1)}{n}\delta, \quad n \gg 1.$$

Since $0 < \delta < 1$, we conclude that

$$\lim_{n\to\infty} \left[1 + \ln\left(\frac{(n+1)}{n}\delta\right) - \frac{(n+1)}{n}\delta\right] = 1 + \ln(\delta) - \delta < 0. \tag{2.15}$$

Thus, if $\lambda = (1+\ln(\delta)-\delta)/2$, then

$$\int_0^{(n+1)\delta} u^n e^{-u}\, du \le n^{(n+1)} e^{-n} e^{n\lambda}, \quad n \gg 1. \tag{2.16}$$

It follows from Stirling's formula that

$$\lim_{n\to\infty} \frac{n^{n+1/2}e^{-n}}{\Gamma(n+1)} = \frac{1}{\sqrt{2\pi}}. \tag{2.17}$$

Combining (2.16) and (2.17) gives

$$\frac{1}{\Gamma(n+1)} \int_0^{(n+1)\delta} u^n e^{-u}\, du \le \left(\frac{n^{(n+1/2)}e^{-n}}{\Gamma(n+1)}\right) n^{1/2} e^{n\lambda} \to 0 \quad \text{as } n \to \infty. \tag{2.18}$$

Finally, we conclude from (2.11), (2.12) and (2.18) that

$$\lim_{n\to\infty} \operatorname{Prob}\{X_n \le X_0 K^n\} = 1, \tag{2.19}$$

and the proof of (2.4) is complete.

Example 1. We now show how to choose K to optimally estimate values of a realization during an extinction event. For this we let $b = 2.05$ in (1.10) and find that the geometric mean satisfies

$$e^{\mathrm{E}(\ln(l))} = \frac{2.05}{e} = 0.754 < 1, \tag{2.20}$$

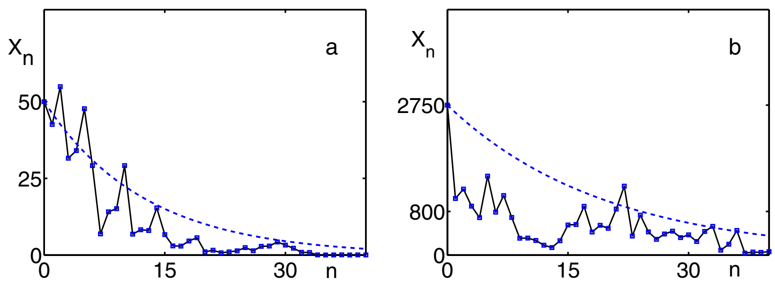

FIGURE 2. (a) Example 1 extinction of a realization (solid curve) of (1.1), (1.10) when $(b, K, X_0) = (2.05, \exp(-0.08n), 50)$. The dashed curve is the upper bound $50 \exp(-0.08n)$ in the prediction $\text{Prob}\{X_n \le 50\exp(-0.08n)\} = 1/\Gamma(n)\int_{0.79784n}^{\infty} u^{n-1}\exp(-u)\,du$, $n \ge 1$. (b) Extinction of a realization of (1.1), (1.10) when $(b, K, X_0) = (2.58, .96, 2750)$. These parameters are from Example 2, where we analyze the Kenyan lion extinction. Dashed curve is the upper bound $X_0K^n = 2750(0.96)^n$ in the prediction $\text{Prob}\{X_n \le 2750(0.96)^n\} = 1/\Gamma(n)\int_{0.9895n}^{\infty} u^{n-1}\exp(-u)\,du$ for all $n \ge 1$.

hence realizations of (1.1) must go extinct (with probability one) as $n \to \infty$. Next, because the right side of (2.4) is independent of X_0, we arbitrarily set $X_0 = 50$ and (2.4) reduces to

$$\text{(2.21)} \quad \text{Prob}\{X_n \le 50K^n\} = \frac{1}{\Gamma(n)} int_{n\ln(2.05/K)}^{\infty} u^{n-1}\exp(-u)\,du \to 1 \quad \text{as } n \to \infty.$$

Now suppose that we want at least 85 percent accuracy in the value of realizations of (1.1) for generation numbers $n \ge 25$. For this we find that the value $K = \exp(-.08)$ gives

$$\text{(2.22)} \quad \text{Prob}\{X_n \le 50\exp(-.08n)\} = \frac{1}{\Gamma(n)}\int_{0.79784n}^{\infty} u^{n-1}\exp(-u)\,du \ge 0.85 \ \forall n \ge 25.$$

It follows from (2.22) that

$$\text{(2.23)} \quad \text{Prob}\{X_{25} \le 4.1\} = 0.85 \text{ and } \text{Prob}\{X_{30} \le 2.1\} = 0.872.$$

Thus, as n increases from $n = 25$, the values of realizations decrease with ever improving accuracy. Figure 2 shows the extinction of a realization when $(b, K, X_0) = (2.05, \exp(-0.08), 50)$. The dashed curve is the dynamic upper bound $50\exp(-0.08n)$ in (2.22).

Example 2. The Kenyan lion extinction. A 2009 report by the Kenya Wildlife Service states that the country's lion population decreased from 2750 to 2000 since 2002. This loss is attributed to climate change, habitat destruction, disease and conflict with humans. The report projects that the lions may be extinct in 20 years. To analyze this data we set $X_0 = 2750$ and N=7 in (1.12) and solve $X_7 \sim 2750(b/e)^7 = 2000$. This gives $b = 2.58$ Following Example 1, we choose $K = 0.96$ to give 85 percent accuracy at $n = 32$, i.e., 25 years from now. Thus, (2.4) becomes

$$\text{Prob}\,\{X_n \leq (0.96)^n X_0\} = \frac{1}{\Gamma(n)} \int_{\log(2.58/0.96)n}^{\infty} u^{n-1} \exp(-u)\, du$$
$$\text{for all } n \geq 1.$$

It follows from this that $\text{Prob}\,\{X_{32} \leq 745\} = 0.85$, hence we predict, with 85 percent certainty, that less than 745 lions will remain in 25 years. The Kenyan report states that 280 lions were lost between 2004 and 2009, an average of 56 per year. At this rate 600 lions will be left 25 years later in 2034, an estimate which compares favorably with our prediction. Both estimates are in contrast with the warning that the lion population may disappear altogether in 20 years. Finally, we note that if we had chosen 90 percent, or 95 percent accuracy, our estimates give similar predictions.

3. Discussion and future studies. In this paper we developed methods to predict the values of realizations of (1.1) during extinct or runaway growth type events. The results given in Theorem 2.1 were proved under the assumption that the growth rates in (1.1) are identically distributed, independent, uniform random variables. An important way to extend these results is to remove the requirement that the growth rates are identically distributed. Instead it may be physically more realistic to assume that the the pdf of growth rate l_n is a function of generation number n. In Example 3 we show how to apply this idea to the evolution of a virus.

The lethal mutagenesis mechanism for virus extinction. On January 5, 2010, the New York Times (page D4) published an article by Zimmer [**19**] which describes a new experimental approach, called 'lethal mutagenesis,' which may cause a virus to go extinct. The basic

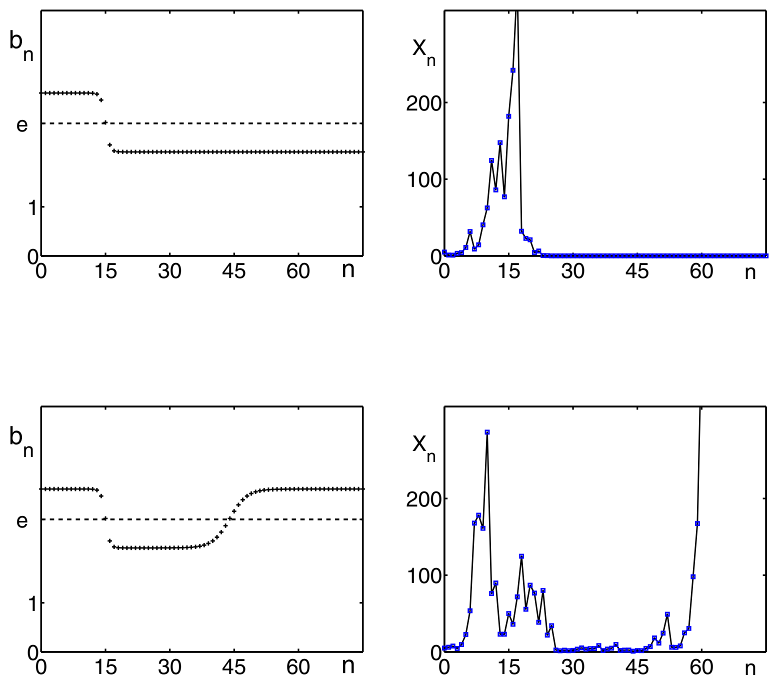

FIGURE 3. Two realizations of (1.1) when the growth rate pdf is given by (1.10). Here $X_0 = 5$, $b = 3.65 > b_{crit} = e$ and runaway growth occurs for $0 \leq n \leq 14$. At the critical generation number $n^* = 15$, b is reset to $b = 2.05 < b_{crit}$ and each realization goes extinct, i.e., $X_n \to 0$ as $n \to \infty$, in spite of the counterintuitive fact that the mean satisfies $\mathrm{E}(X_n) = 5(b/2)^n = 5(1.025^n) \to \infty$ as $n \to \infty$. The observation that the first realization goes extinct much earlier than the second is due to the wide variability in realizations. This wide variability is due to the uncertainty in the growth rate l.

idea behind this approach is that if a virus is forced to radically increase its rate of mutation, then the number of 'good offspring' necessary for propagation of the virus will decrease. In turn, it is thought that this will force the growth rate of the virus population to decrease below a level of sustainability, and that the virus will go extinct [**1, 2**]. Our goal is to incorporate these ideas into (1.1), and investigate the resultant behavior of realizations. For this, we assume that uncertainty in the growth rate is governed by a probability distribution which is dependent on the generation number n. As a first step, we extend (1.10) and assume that l_n in (1.1) is a uniform random variable whose pdf is

$$f_n(l) = \begin{cases} 1/b_n & \text{when } 0 < l \le b_n, \\ 0 & \text{when } l \notin (0, b_n], \end{cases} \tag{3.1}$$

where b_n is a function of n. It follows from (3.1) that the mean growth rate is

$$\mathrm{E}(l_n) = \frac{b_n}{2}, \quad n \ge 1. \tag{3.2}$$

Thus, the mean growth rate is now allowed to vary with n, as required by the hypothesis of lethal mutagenesis. Below, we investigate the behavior of realizations of (1.1)–(3.1) for two fundamentally different choices of b_n. The outcome of these scenarios is illustrated in Figure 3.

Scenario I. In accordance with the present theory of lethal mutagenesis, we assume that the mutation rate is sufficient to cause the mean growth rate $\mathrm{E}(l_n) = b_n/2$ to decrease to a level below which the population cannot sustain itself. Thus, in accordance with theoretical predictions of the previous sections, we assume that, as the generation number n increases, the parameter b_n decreases from a level above the critical value e where runaway growth is predicted, to a level below e. For simplicity, we assume that b_n satisfies (Figure 3, first row)

$$b_n(l) = (e + 0.6 \tanh(15 - n)), \quad n \ge 1. \tag{3.3}$$

For this choice of b_n we find that

$$\mathrm{E}(l_n) = \frac{b_n}{2} \ge \frac{e - 0.6}{2} \approx 1.059 \quad \text{for all } n \ge 1. \tag{3.4}$$

Thus, because the l_n are assumed to be independent, the mean of X_n satisfies

$$\mathrm{E}(X_n) = \left(\prod_{i=1}^{n} \mathrm{E}(l_i) \right) X_0 \ge (1.059)^n X_0 \longrightarrow \infty \quad \text{as } n \to \infty. \tag{3.5}$$

Thus, as we described in Section 1, one might be tempted to predict that realizations of (1.1) will be unbounded, and runaway growth must occur. However, as Figure 3 (first row, second column) shows, this is not what happens.

Scenario II. In accordance with the present theory of lethal mutagenesis, we assume that the mutation rate is sufficiently large that the mean growth rate decreases as generation number n increases. In particular, we assume that b_n decreases from a level above the critical value e where runaway growth is predicted to a level below e where the geometric mean will have an effect. For simplicity we assume that b_n satisfies

$$b_n(l) = \begin{cases} (e + 0.6\tanh(15 - n))0 & \text{when } l \leq n \leq 44, \\ (e + 0.6\tanh(0.5(n - 45)))0 & \text{when } n \geq 45. \end{cases} \tag{3.6}$$

(1) Sachs [**17** points out that (see p. 36) "since 1970 the population has risen from 3.7 billion to 6.9 billion, and continues to 9 increase at a rate of 85 million per year. In some regions food production per person has declined, e.g., in sub-Sahara Africa. In India the doubling of the population has absorbed all of the increase in grain production." Also on p. 36 –"Forecast of 7 billion around 2012, and 9 billion by 2046." We must produce more food, but simultaneously stabilize pop growth."

Include the virus application from nyt. *Alternative approaches.* Ludwig employs Bayesian techniques and also catastrophe theory ideas, to analyze extinction probabilities in ecological models [**11, 12**].

REFERENCES

1. J.J. Bull, R. Sanjun and C.O. Wilke, *Theory of lethal mutagenesis for viruses*, J. Virol. **81** (2007), 2930–2939.

2. ———, *Lethal mutagenesis*, in *Origin and evolution of viruses*, 2nd ed., E. Domingo, C.R. Parrish and J.J. Holland, eds., Elsevier, New York, 2008.

3. L. Devroye, *Non-uniform random variate generation*, Springer-Verlag, New York, 1986.

4. C. Doering, *Modeling complex systems*: *Stochastic processes, stochastic differential equations, and Fokker-Planck equations*, The Proceedings of the 1990 Complex Systems Summer School, Santa Fe, New Mexico.

5. C. Doering, K.V. Sargsyan and L.M. Sander, *Extinction times for birth-death processes*: *Exact results, continuum asymptotics, and the failure of the Fokker-Planck aproximation*, Multiscale Mod. Sim. **3** (2005), 283–299.

6. J. Fieberg and S. Ellner, *When is it meaningful to estimate an extinction probability?*, Ecology **81** (2000), 2040–2047.

7. B. Holmes, *Earth*: *The comeback*, Science News, October 3 (2009), 32–35.

8. *Human impact report*: *Climate Change–The anatomy of a silent crisis*, Global Humanitarian Forum, London, 2009.

9. M. Hume, *The true meaning of climate change*, New Scientist 14 Sept. (2009), 28–29.

10. R.C. Lewontin and D. Cohen, *On population growth in a randomly varying environment*, PNAS **62** (1969), 056–1060.

11. D. Ludwig, *Uncertainty and the assessment of extinction probabilities*, Ecol. Appl. **6** (1996), 1067–1076.

12. ———, *Is it meaningful to estimate the probability of extinction*, Ecology **80** (1999), 298–310.

13. T.R. Malthus, *An essay on the principle of population*, 1798 First Edition, JH. Johnson Pub., London, 1798.

14. A. Robock and B. Toon, *Local nuclear war, global suffering*, Scientific American, Jan. 2010, 74–81.

15. K. Rogers, *Scientists report on explosive growth of invasive quagga mussels*, Las-Vegas Review Journal-Journal, Jan. 14, 2009.

16. Kenyan Wildlife Service, Press Release, August 17, 2009.

17. J.D. Sachs, *Transgressing planetary boundaries*, Scientific American, Dec. 2009, 2008, page 36.

18. C.H. Sekercioglu, S.H. Schneider, S.H. Fay and J.P. Loarie, *Climate change, elevational range shifts, and bird extinctions*, Comservation Biology **22** (2008), 111–119.

19. C. Zimmer, *Using a virus's knack for mutation to wipe it out*, The New York Times, Jan. 5, 2010, p. D4.

Department of Mathematics, University of Pittsburgh, Pittsburgh PA 15260
Email address: troy@math.pitt.edu