Evaluating Persistence Times in Populations that are Subject to Local Catastrophes

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Abstract: The birth-death process is a familiar tool in modelling populations which are subject to demographic stochasticity. However, many populations are also subject to one or more forms of local 'catastrophe' (a term usually taken to mean any population decrease of size greater than one). Natural disasters, such as epidemics, and migration to other populations, are all examples of local catastrophes. The birth, death and catastrophe process is an extension of the birth-death process that incorporates the possibility of reductions in population of arbitrary size. We will consider a general form of this model, in which the transition rates are allowed to depend on the current population size in a completely arbitrary matter. The linear case, where the transition rates are proportional to current population size, has been studied extensively. In particular, extinction probabilities, the expected time to extinction (persistence time) and the distribution of the population size conditional on non-extinction (the quasi-stationary distribution) have been evaluated explicitly. However, whilst all of these characteristics are of interest in the modelling and management of populations, processes with linear rate coefficients represent only a very limited class of models, and indeed it is difficult to imagine instances where catastrophe events would occur at a rate proportional to the population size. Our model addresses this difficulty by allowing for a wider range of catastrophic events. Despite this generalisation, explicit expressions can still be found for persistence times.

Keywords: *Hitting times; Extinction times; Population processes*

1. INTRODUCTION

Accounting for catastrophic events has become an important component in stochastic population modelling, particularly in ecological applications, but also in an array of other fields, including economics, chemistry and telecommunications. In the context of population processes, catastrophes are sudden declines in population, typically of a size greater than a single individual. According to Shaffer (1981) and others, such catastrophes are one of the primary sources of variation in the abundance of species. Mangel and Tier (1993), for example, discuss the use of birth, death and catastrophe processes in modelling the number of occupied habitat patches in a metapopulation. See Shafer (2001) for a review of the significance of catastrophes in ecological modelling.

Of primary importance in most applications is the effect of catastrophes on the persistence of a population, and in particular on the expected time to extinction. Recent work, beginning with Brockwell, et al. (1982), discusses extinction probabilities, conditions for certain extinction and expected extinction times, in a variety of different cases. Here, we examine a general birth, death and catastrophe model that permits an entirely arbitrary dependence of the transition rates on the current population size, as well as an arbitrary (but constant) jump size distribution. Our main result is a theorem giving an explicit expression for the expected extinction time for

processes that conform to this model. We illustrate our result with several examples.

2. THE MODEL

Markov chains are the simplest mathematical models for random phenomena that evolve over time. Their structure is sufficiently simple that one can say a great deal about their behaviour, yet, at the same time, the class of Markov chains is rich enough to serve in many applications. Markov chains have proved particularly effective in biological contexts. Here we shall assume that $X(t)$ is the number in the population at time t, and suppose that $(X(t), t \geq 0)$ is a continuous-time Markov chain taking values in $S = \{0, 1, \dots\}$. Let $f_i(> 0)$ be the rate at which the population size changes when there are i individuals present, and suppose that, when a change occurs, it is a birth with probability $a(> 0)$ or catastrophe of size k (the removal of k individuals) with probability d_k, $k \geq 1$. (Simple death events are to be interpretted as catastrophes of size 1.) Assume that $d_k > 0$ for at least one $k \geq 1$ and that $a + \sum_{k \geq 1} d_k = 1$. Thus, the process has transition rates Q given by

$$
q_{ij} = \begin{cases}
f_i \sum_{k \geq i} d_k, & j = 0, \ i \geq 1, \\
f_i d_{i-j}, & j = 1, 2, \dots i - 1, \ i \geq 2, \\
-f_i, & j = i, \ i \geq 0, \\
f_i a & j = i + 1, \ i \geq 0, \\
0, & \text{otherwise.}
\end{cases}
$$

$$(1)$$

Notice, in particular, that $q_{0j} = 0$, $j \geq 0$, and that $q_{i0} > 0$ for at least one $i \geq 1$. Thus, the sole absorbing state 0, corresponding to population extinction, is accessible from $\{1, 2, \dots\}$ (an irreducible class).

The special case $f_i = \rho i$, where $\rho(> 0)$ is a per-capita transition rate, was studied by Brockwell (1985), Pakes (1987) and Pollett (2001). Brockwell's model requires that the rate at which catastrophes occur is proportional to the number of individuals present (as is the birth rate). Such a relationship would be appropriate, for example, in situations where each individual in the population triggers catastrophic epidemics at a certain rate. In contrast, models of the general form (

Whilst our model is quite general, it does have limitations. Firstly, it is frequently useful to separate death and catastrophe events, and to assign different rate functions to births, deaths and catastrophes, as in Mangel and Tier (1993) (note that in that work, the state of the process is the number of occupied patches in a metapopulation). An important special case, which we are presently studying, has $q_{ij} = \lambda i$, for $j = i - 1$ and $i \geq 1$, and $q_{ij} = \rho d_{i-j}$, for $j = 1, \dots, i - 1$ and $i \geq 2$, so that deaths occur at per-capita rate $\lambda(> 0)$, while catastrophes occur at

points of Poisson process with rate $\rho(> 0)$, independent of the population size. Another drawback of the present model is that the catastrophe size distribution does not depend on the number of individuals present. For example, it rules out two special cases. The first, and most important, describes catastrophic events that affect each and every individual in the population, and each individual is removed independently with some fixed probability p. Thus, when there are i individuals present, the size of a catastrophe has a binomial $B(i, p)$ distribution. The second case is where all catastrophe sizes are equally likely, so that the catastrophe size has a uniform distribution on the set $\{1, 2, \dots, i\}$; uniform catastrophes are not so relevant in biological applications. Both cases have been discussed in previous mathematical analyses; see, for example, Brockwell, et al. (1982).

A final important aspect of the model relates to 'total catastrophes', events that wipe out the population completely. The number of deaths attributed to a catastrophe is always limited by the current population, since the size of a population can never be negative. In other words, while a certain severity of catastrophe might be just enough to wipe out a population, exactly the same effect (extinction) would be produced by a catastrophe that was, say, twice as severe. It is a feature of our model that these 'larger-than-population-size' catastrophes still contribute to the rate of total catastrophes. Notice from (

3. EXTINCTION PROBABILITIES

The probability of extinction does not depend on the event rates $(f_i, i \geq 1)$, because the jump chain (the discrete-time chain that records the sequence of states visited) is the same in all cases. It was shown by Pakes (1987) that the probability of extinction α_i, starting with i individuals, is 1 for all $i \geq 1$ if and only if the drift D (drift *away* from 0), given by

$$
D = a - \sum_{i \geq 1} i d_i = 1 - \sum_{i \geq 1} (i + 1) d_i,
$$

is less than or equal to 0. Note that the process is said to be *subcritical*, *critical* or *supercritical* according as $D < 0$, $D = 0$ or $D > 0$ (where D satisfies $-\infty \leq D \leq 1$). In the latter case extinction is of course still possible, and the extinction probabilities can be expressed in terms of the probability generating function

$$
d(s) = a + \sum_{i \geq 1} d_i s^{i+1}, \quad |s| < 1. \qquad (2)
$$

It follows from Theorem 4 of Ezhov and Reshetnyak (1983) (see also Pakes (1987)) that, when $D > 0$,

$$
\sum_{i \geq 1} (1 - \alpha_i) s^i = \frac{Ds}{d(s) - s}.
$$