

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 manner. 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

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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 interpreted 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

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

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 (1) may provide a suitable approximation to the behaviour of populations (or metapopulations) that are evenly spread across their environment, and that are subject to 'localised' catastrophes. If we define a localised catastrophe to be one that affects only nearby members of a population, such catastrophes will often have size distributions that are indeed independent of the population size, and will not typically affect the entire population, except when the population is small. Our purpose here is to evaluate the expected time

to extinction for this general model, thus extending Brockwell's results for the linear case.

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 (1) that total catastrophes occur at rate $q_{i0} = f_i \sum_{k \geq i} d_k$ when the population size is i , which is the the rate coefficient f_i multiplied by the probability of a catastrophe of a size greater than or equal to the current population. In this way, catastrophes that are more than sufficient to wipe out a population are still possible, and contribute to precisely the event that the population jumps directly to zero.

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

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

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

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

Thus, writing $b(s) = d(s) - s$, we see that

$$\sum_{i \geq 1} \alpha_i s^{i-1} = \frac{1}{1-s} - \frac{D}{b(s)}. \quad (3)$$

It is interesting to note that α_i tends to 0 as i tends to ∞ ; roughly speaking, the larger the initial population the less likely the population is to become extinct (in the supercritical case). However, as Pakes (1987) notes, the convergence of α_i to 0 can be very slow. For example, it is easy to show that $\sum_{i \geq 1} \alpha_i$ is finite (and hence α_i decays very quickly) if and only if the *variance* of the catastrophe size distribution is finite.

4. POPULATION EXPLOSIONS

One interesting aspect of the present model is that the process may explode (that is, the population size may reach infinity in a *finite* time). Of course this can only occur in the supercritical case, for as we have already seen, the process hits 0 with probability 1 in the subcritical and critical cases.

It is easy to exhibit explosive behaviour, for imagine that there is no catastrophe component in the model. We obtain the pure-birth process with birth rates $q_{i,i+1} = f_i a$, and this is well known to be explosive if and only if $\sum_{i \geq 1} g_i < \infty$, where $g_i = 1/f_i$. If death transitions are included, that is, $q_{i,i-1} = f_i b$, where $a + b = 1$, then the resulting birth-death process is explosive if and only if $a > b$ (supercritical) and $\sum_{i \geq 1} g_i < \infty$ (apply Theorem 3.2.2 of Anderson (1991)). It might therefore be conjectured

that the general birth, death and catastrophe process is explosive if and only if it is supercritical and $\sum_{i \geq 1} g_i < \infty$. Using the results of Yan and Chen (1986), we have established that this is indeed the case, but we will not give details here.

5. EXPECTED EXTINCTION TIMES

In this section we shall evaluate the expected time to extinction with initial population i . We shall restrict our attention to the subcritical case, where extinction occurs with probability 1.

For a general Markov chain with transition rates $Q = (q_{ij}, i, j \in S)$, whose state space consists of an irreducible class $\{1, 2, \dots\}$ and a single absorbing state 0 that is reached with probability 1, the expected absorption time τ_i , starting in state i , is the minimal non-negative solution to the system of equations

$$\sum_{j \geq 0} q_{ij} z_j + 1 = 0, \quad i \geq 1, \quad (4)$$

with $z_0 = 0$. This result can be found in any text on Markov chains (see, for example, Theorem 3.3.3 of Norris (1997)), and yet it is apparently not widely known to biologists, a problem that is no doubt due to the highly technical nature of many papers on the subject. It is, however, often just a matter of simple arithmetic to evaluate the expected absorption times, and failing that, a host of numerical methods exist—we are merely solving a system of linear equations. In their paper “Four facts every conservation biologist should know about persistence”, Mangel and Tier (1994) implore their readers to use (4): Fact 2 “There is a simple and direct method for the computation of persistence times that virtually all biologists can use”.

We will now address the problem of deriving expected extinction times for the present case, culminating in the theorem stated towards the end of this section. On substituting the transition rates, (4) becomes

$$f_i a z_{i+1} - f_i z_i + f_i \sum_{j=1}^{i-1} d_{i-j} z_j + 1 = 0, \quad i \geq 1,$$

with the empty sum being interpreted as 0 when $i = 1$. This can be written

$$a z_{i+1} - z_i + \sum_{j=1}^{i-1} d_{i-j} z_j + g_i = 0, \quad i \geq 1, \quad (5)$$

where (recall that) $g_i = 1/f_i$. On multiplying by s^i and then summing over i , we find that the generating function $h(s) = \sum_{i=1}^{\infty} z_i s^{i-1}$ of any solution ($z_i, i \geq 1$) to (5) must satisfy $b(s)h(s) - a z_1 +$

$g(s) = 0$, where $g(s) = \sum_{i=1}^{\infty} g_i s^i$. (We delay addressing the question of whether the solution is non-negative.)

We know, from Lemma V.12.1 of Harris (1963), that $e(s) = 1/b(s)$ has a power series expansion with positive coefficients in a neighbourhood of 0. We can identify its radius of convergence. Since $b''(s) = d''(s) > 0$ for $s \in (0, 1)$, b is convex on $(0, 1)$, and, because $b(0) = a (> 0)$ and $b(1) = 0$, the smallest solution σ of $b(s) = 0$ in $(0, 1]$ satisfies $\sigma = 1$ if $D \geq 0$ and $\sigma < 1$ if $D < 0$. Furthermore, $b(s) > 0$ for all $s \in [0, \sigma)$. Therefore, the power series expansion of $e(s)$ has radius of convergence σ . (In the present subcritical case, $\sigma < 1$.) Let us write $e(s) = \sum_{j=0}^{\infty} e_j s^j$, $|s| < \sigma$, where $e_j > 0$, noting that $a = b(0) = 1/e_0$. Letting $\kappa = a z_1$, we obtain

$$h(s) = z_1 + \sum_{i=1}^{\infty} \left(\kappa e_i - \sum_{j=1}^i g_j e_{i-j} \right) s^i,$$

and hence, for $i \geq 2$,

$$z_i = \kappa e_{i-1} - \sum_{j=1}^{i-1} g_j e_{i-1-j}. \quad (6)$$

Now, (e_i) is an increasing sequence. To see this, observe that if we had $g_i = 0$ for all i , then we would have $z_i = \kappa e_{i-1}$ and then, from (5),

$$a e_i - e_{i-1} + \sum_{j=1}^{i-1} d_{i-j} e_{j-1} = 0, \quad i \geq 1, \quad (7)$$

with the empty sum being interpreted as 0 when $i = 1$. Hence, (e_i) satisfies

$$a(e_i - e_{i-1}) = \sum_{j=1}^{i-1} d_{i-j}(e_{i-1} - e_{j-1}) + e_{i-1} \sum_{j=i}^{\infty} d_j, \quad i \geq 1. \quad (8)$$

Since $e_0 = 1/a > 0$ and $d_j > 0$ for at least one $j \geq 1$, a straightforward inductive argument shows that (e_i) is increasing.

Therefore, referring to (6), (z_i) is the difference of two non-negative increasing sequences. Thus, in order to ensure that (z_i) itself is non-negative, we require $\kappa \geq \sup_{i \geq 1} h_i$, where

$$h_i = \frac{1}{e_i} \sum_{j=1}^i g_j e_{i-j} = \sum_{j=1}^i g_j \left(\frac{e_{i-j}}{e_i} \right). \quad (9)$$

The minimal solution is then obtained on setting $\kappa = \sup_{i \geq 1} h_i$.

Since (e_i) is increasing, we have $0 < e_{i-j}/e_i \leq 1$ for all $i \geq j \geq 0$. Moreover, because σ is the radius of convergence of $\sum_{j=0}^{\infty} e_j s^j$, we have $\sigma = \lim_{i \rightarrow \infty} e_{i-1}/e_i$, whenever this limit exists, implying that $e_{i-j}/e_i \rightarrow \sigma^j$ for each j . Hence, formally, $h_i \rightarrow g(\sigma)$. Once we prove that this limit exists and equals $\sup_{i \geq 1} h_i$, we may set $\kappa = g(\sigma)$ to obtain the minimal non-negative solution to (5).

To achieve this, we will draw further on branching process theory. Since $e(s)$ has a power series expansion with positive coefficients, then so does

$$\pi(s) = a \pi_1 \int_0^s \frac{du}{b(u)}, \quad |s| < \sigma.$$

Indeed, writing $\pi(s) = \sum_{i \geq 1} \pi_i s^i$, it is easy to see that $\pi_i/\pi_1 = a e_{i-1}/i$, $i \geq 1$. However, the coefficients (π_i) form a stationary measure on $\{1, 2, \dots\}$ for the Markov Branching Process with offspring distribution $(q_i, i \geq 0)$, where $q_0 = a$, $q_1 = 0$ and $q_i = d_{i-1}$ for $i \geq 2$ (refer to the corollary of Theorem V.12.2 of Harris (1963)). Theorem 1(e) of Yang (1973) then gives $i \pi_i \sigma^i \uparrow a \pi_1 / (1 - d'(\sigma))$, as $i \rightarrow \infty$, whenever $D \neq 0$ (note that $d'(\sigma) < 1$ since $b'(\sigma) < 0$ when $D \neq 0$). Consequently, $e_i \sigma^{i+1} \uparrow 1/(1 - d'(\sigma))$. Thus, by the monotonicity of this limit, $e_{i-1}/e_i \leq \sigma$ and hence $e_{i-j}/e_i \leq \sigma^j$ for $j = 1, \dots, i$. Furthermore, $e_{i-j}/e_i \rightarrow \sigma^j$ as $i \rightarrow \infty$. Applying the Dominated Convergence Theorem to (9) shows that if $g(\sigma) < \infty$, then $h_i \rightarrow g(\sigma)$ and hence $\sup_{i \geq 1} h_i = g(\sigma)$ because $h_i \leq g(\sigma)$. On the other hand, Fatou's Lemma always gives $\liminf_{i \rightarrow \infty} h_i \geq g(\sigma)$, so if $g(\sigma) = \infty$, then $\sup_{i \geq 1} h_i = \infty$. We have therefore proved the following result.

Theorem For the subcritical birth, death and catastrophe process with transition rates (1), let $(e_i, i \geq 0)$ be the coefficients of the power series expansion of $e(s) = 1/(d(s) - s)$, $|s| < \sigma$, where $d(s)$ is given by (2), and $\sigma (< 1)$ is the smallest solution of $d(s) = s$ in $(0, 1]$. Then, the expected extinction time τ_i , starting in state i , is finite if and only if $\kappa := \sum_{i \geq 1} \sigma^i / f_i < \infty$, in which case $\tau_0 = 0$ and

$$\tau_i = \kappa e_{i-1} - \sum_{j=1}^{i-1} e_{i-1-j} / f_j, \quad i \geq 1. \quad (10)$$

Thus, equations (7) and (10) provide a direct method for evaluating persistence times for a wide range of population processes. Moreover, each of the conditions of the theorem will frequently be satisfied in practice: the importance of catastrophes in this context is that they often contribute, over long periods of time, to a downward drift in the population (so $D < 0$ and the process is subcritical), and the quantity κ will be finite in many situations, too,

including most of the examples treated in the next section.

We conclude this section with some remarks on the critical and supercritical cases, both of which have $\sigma = 1$. Our theorem is certainly valid in the critical case provided that the variance of the catastrophe size distribution is finite ($d''(1-) < \infty$): the expected extinction times are all finite if and only if $\kappa := \sum_{i \geq 1} 1/f_i < \infty$, in which case (10) holds. This is true because, as $i \rightarrow \infty$, $e_{i-j}/e_i \rightarrow 1$ (from Theorem 1(c) of Yang (1973)). (The infinite variance case is mathematically delicate, and we will not pursue it further here.) In the supercritical case, where there is a probability α_i of extinction, starting in i , which is *strictly less than 1* (and therefore the expected extinction times are infinite), it is possible to evaluate expected extinction times *conditional on* extinction occurring. This can be done by interpreting our result for the (subcritical) birth, death and catastrophe process with transitions rates $\bar{q}_{ij} = q_{ij}\alpha_j/\alpha_i$, and following the programme laid out in Walker (2001).

6. EXAMPLES

First let us examine the linear case studied by Brockwell (1985). This has $f_i = \rho i$, where $\rho > 0$. So, $g(s) = -\log(1-s)/\rho$, $|s| < 1$, implying that $g(\sigma)$ is finite whenever $\sigma < 1$. Setting $\kappa = -\log(1-\sigma)/\rho$, we get from (10)

$$\tau_i = \frac{1}{\rho} \left(e_{i-1} \log \left(\frac{1}{1-\sigma} \right) - \sum_{j=0}^{i-2} \frac{e_j}{i-j-1} \right),$$

for $i \geq 1$. This is equivalent to

$$\sum_{i=1}^{\infty} \tau_i s^{i-1} = \frac{1}{\rho b(s)} \log \left(\frac{1-s}{1-\sigma} \right), \quad |s| < \sigma,$$

which is equation (3.1) of Brockwell (1985).

Further examples of the subcritical birth, death and catastrophe process for which the expected extinction times are finite include the following cases. In the case where events occur at a constant rate $f_i = \rho > 0$, and hence where the rate at which catastrophes occur is independent of the population size (for example, some environmental catastrophes), we find that $\kappa\rho = \sigma/(1-\sigma)$. A second example is where $f_i = \rho i(i+1)$, so that events occur at a rate proportional to the number of interactions between individuals, giving

$$\kappa\rho = 1 - \left(\frac{1-\sigma}{\sigma} \right) \log \left(\frac{1}{1-\sigma} \right).$$

If $f_i = \rho\beta^{i-1}$, where $\rho, \beta > 0$, then the expected extinction times are finite only if $\sigma < \beta$, in which

case $\kappa\rho = \beta\sigma/(\beta-\sigma)$. This latter example generalises the constant rate case, where $\beta = 1$, while remaining analytically tractable.

Explicit results can be obtained in cases where the catastrophe size follows a geometric law. Geometric distributions occur in circumstances where we are waiting for the first ‘success’ in a sequence of independent trials. In the context of population processes with catastrophes, a geometric catastrophe size distribution would correspond to the case where the decline in the population is halted as soon as any individual survives the catastrophic event. This may be appropriate for some forms of catastrophic epidemics. Suppose then that catastrophes follow a geometric law: $d_i = b(1-q)q^{i-1}$, $i \geq 1$, where $b(> 0)$ satisfies $a+b=1$, and $0 \leq q < 1$. Here, q is the probability that the ‘next’ individual will succumb to the catastrophe. The simple birth-death process with linear birth and linear death rates is recovered on setting $q = 0$. It is easy to see that $D = a-b/(1-q)$, and so $D < 0$ or $D \geq 0$ according as $c > 1$ or $c \leq 1$, where $c = q + b/a$. We also have

$$\begin{aligned} b(s) &= \frac{(b+qa)s^2 - (1+qa)s + a}{1-qs} \\ &= \frac{a(1-s)(1-cs)}{1-qs}, \end{aligned}$$

and hence if $D < 0$, then $\sigma = 1/c (< 1)$. The coefficients of the power series $1/b(s) = \sum_{j=0}^{\infty} e_j s^j$ are easily evaluated using partial fractions. If $D < 0$ (or indeed if $D > 0$), then

$$e_j = \frac{1-q-(c-q)c^j}{a(1-c)}, \quad j \geq 0.$$

We may evaluate τ_i by substituting these expressions into (10). If, for example, $f_i = \rho\beta^{i-1}$, where $\rho, \beta > 0$, then if $\beta = 1$,

$$\tau_i = \frac{1+(1-q)(i-1)}{\rho(b-a(1-q))}, \quad i \geq 1,$$

while if $\beta \neq 1$, the expected extinction times are finite only if $\beta > a/(b+qa)$, in which case

$$\tau_i = \frac{1-q-(\gamma-q)\gamma^{i-1}}{\rho(b-a(\gamma-q))(1-\gamma)}, \quad i \geq 1,$$

where $\gamma = 1/\beta$.

The relationship between the expected extinction times τ_i and the rate coefficients f_j , $j < i$, is described by equation (10). The examples given in Figure 1 demonstrate a range of qualitatively different relationships between the initial state of the population i and expected extinction times. In each of these cases, the catastrophe size follows the same geometric distribution. First, let $f_j = \rho\beta^{j-1}$, and

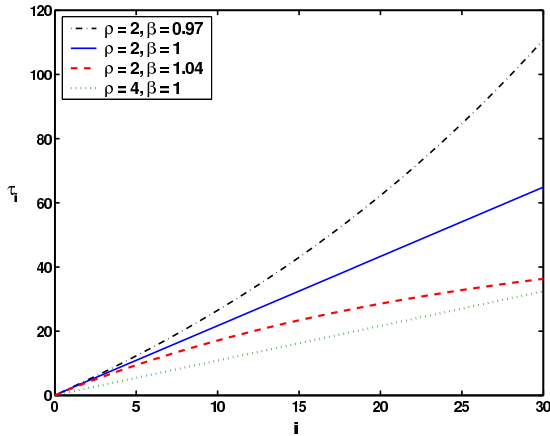


Figure 1: Expected extinction times τ_i for several processes with rate coefficients $f_j = \rho\beta^{j-1}$. An increase in f_j will produce a corresponding decrease in times τ_i , for $i > j$.

let $\rho = 2$ be fixed. For $\beta < 1$, $\beta = 1$ and $\beta > 1$, and hence for f_j decreasing, constant and increasing with j (respectively), the rate of change in τ_i is increasing, constant and decreasing with i (respectively). Then, fixing $\beta = 1$, by altering ρ by a fixed factor, 2, we alter the rate of change in τ_i by the same factor, but in the opposite direction.

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