On the life-time of a size-dependent branching process

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In this study I will look at some simple size-dependent branching processes with varying carrying capacities. The shape of the (deterministic) production functions is decisive when it comes to certain modes of extinction, such as the growth-catastrophe behavior and the response to sudden shocks.

It is well known that most size-dependent branching models have a life time whose expectation is exponential in the carrying capacity K. A study by Hamza *et al.* (*Journ. Math. Biol.* 2016) exhibits an explicit expression for the dependence in a very simple, but illustrative case. One of the conclusions drawn is that extinction rarely depends on demographic variation in a fixed environmental setting: the life time is usually extremely long.

The main focus here is, then, on the case with fluctuating environment.

The functions studied are

(Beverton-Holt)

$$\frac{rz}{1+\frac{z}{K}}$$

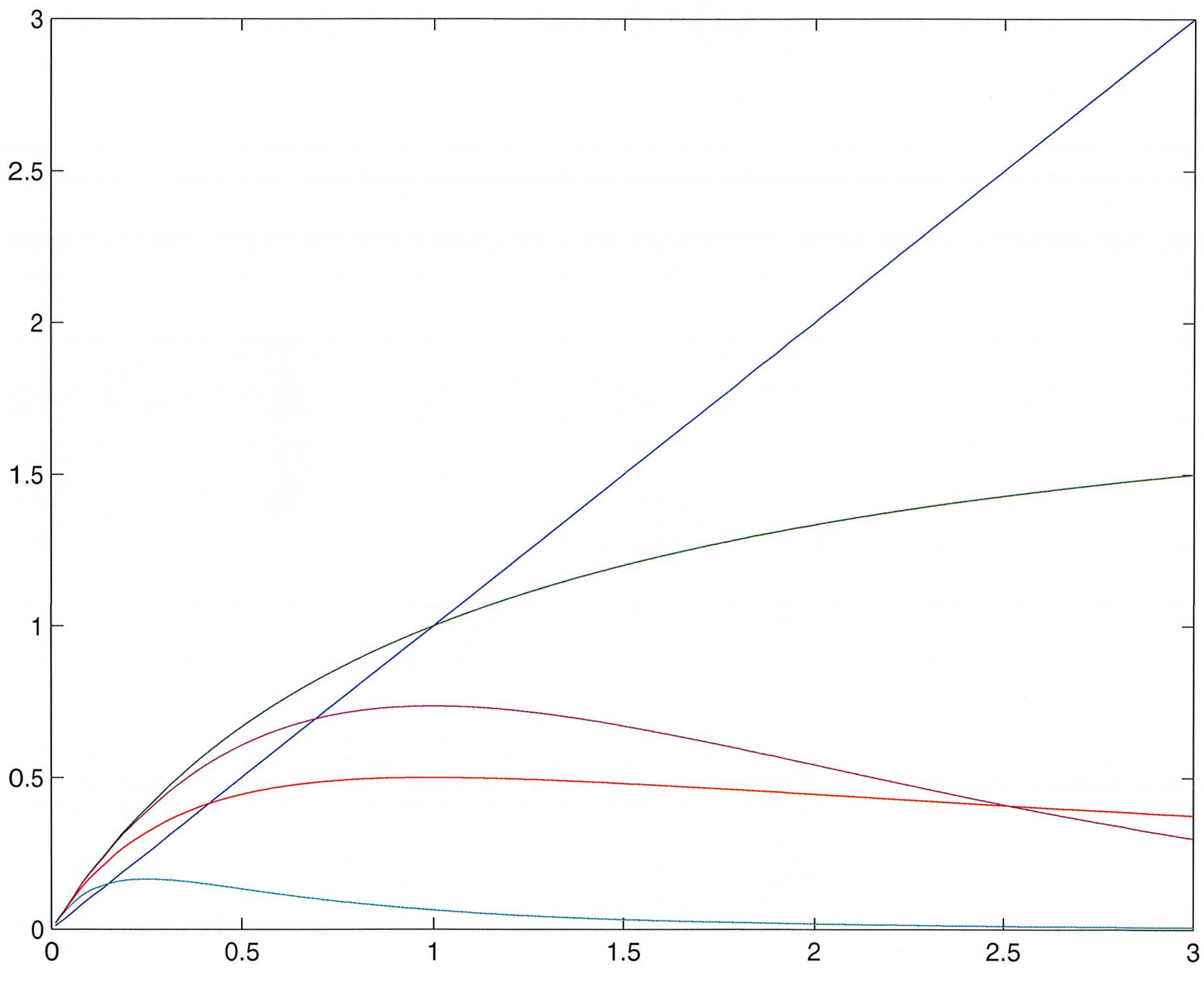
(Hassell)

$$\frac{rz}{(1+\frac{z}{K})^b}$$

(Ricker)

$$z\exp(r-\frac{z}{K})$$

where z is the population size, K the carrying capacity, r or e^r the mean growth rate at small sizes, $b \geq 1$ is a parameter.



Production functions

B-H: $\frac{2z}{1+z}$

Hassell (2): $\frac{2z}{(1+z)^2}$

Ricker: $2z\,e^{-z}$

Hassell (5): $\frac{2z}{(1+z)^5}$

We notice, for instance, that the Beverton-Holt model and the Hassell models with b small, do not react as dramatically to over-population as the Ricker model does.

In the size-dependent discrete-time branching process studied by Hamza *et al.* we have Z_t particles at time t. At time $t+1$ each of them, independently, with probability $\frac{K}{K+Z_t}$ gives rise to 2 offspring and dies. With probability $1 - \frac{K}{K+Z_t}$ it dies without offspring.

The mean of the process at time $t+1$, given that we have Z_t particles at time t is

$$\frac{2Z_t}{1 + \frac{Z_t}{K}}.$$

If we start from very low values there is a chance that the process goes extinct fast. But if not, it will soon (after about $\log(K)$ steps) stabilize around the attracting fixed point K. The time of descending below the level $\frac{K}{2}$ has expectation at least $\exp(cK)$ where $c = \frac{1}{96}$.

The calculations rely on a large deviations result for binomial variables due to Svante Janson (1994). The process close to K may also be approximated by a linear autoregressive process (Klebaner and Nerman (1994)). The exit time for the AR approximation is even longer, of the order of $\exp(\frac{3}{32}K)$ (Jung 2008, 2013)

Using one of the other maps to define the probabilities does not change the picture very much. In the Ricker case we would take $r = \log 2$ and the probability of offspring $= \exp(-\frac{Z_t}{K})$. The fixed point is then rK.

The AR approximation leaves the level $\frac{rK}{2}$ after $\exp(0.0785K)$ steps, while the lower bound, by Janson, is about $\exp(0.0105K)$. Again, this is a very large number even for biologically moderate K.

While fixed K in all our cases always lead to life times exponential in K, large values of r may blur the impression since the asymptotics sets in only for very large carrying capacities.

Let r in the Ricker model be 4, say. The deterministic model is chaotic; the quotient between the largest and smallest value is in the millions. Regardless of our assumptions on the branching mechanism, the probability of immediate extinction from the level $20K$ is about $(1 - \exp(-20))^{20K}$ which is about $1 - 20K \exp(-20)$ for moderate K.

Let me now assume that the carrying capacities K_t form an i.i.d. sequence of random variables on the whole positive real line $(0, \infty)$. The real-valued process, obtained by iteration of these random mappings, is then positive recurrent (Gyllenberg *et al.* 1994).

The first question that I would like to investigate is resilience to sudden moderate shocks. Let us imagine that the process is subject to a drop in carrying capacity, to a tenth of its former value, say. Will it be able to survive the shock? This will depend on the form of our production function.

The branching mechanism is as follows. Again let Z_t be the number of individuals at time t. They have offspring, independently, conditional on the carrying capacity sequence, with a probability of

$$\frac{K_{t+1}}{K_{t+1} + Z_t}, \quad \frac{1}{(1 + \frac{Z_t}{K_{t+1}})^b}, \quad \exp(-\frac{Z_t}{K_{t+1}})$$

in our different cases. Otherwise, they die without offspring. The offspring distribution is assumed given, with mean r, r, and e^r, respectively.

Beverton-Holt case: Probability of extinction is only about $\exp(-\frac{K_t}{11})$.

In the Ricker case the probability of extinction is appreciable for moderately large K_t, it is $(1-e^{-10r})^{rK_t}$. The value is about .51 for $r = \log 2$ and $K_t = 1000$.

The Hassell models lie in-between, extinction is probable for small K_t.

The nature of these one-dimensional models is such that, if they survive, they adapt to changes in the environment immediately, so that several "equally bad years" are no worse than the first shock. Overpopulation is detrimental as well: the discrete-time model may not be able to limit excessive growth (as opposed to models in continuous time) until it is too late.

Next, I will show that the extinction by a growth-catastrophe scenario may in some cases lead to shorter than exponential life times. The mechanism is roughly the same as we saw earlier in the Ricker model when K was constant and r was large.

For the Beverton-Holt model excessive growth is not immediately dangerous: The probability of extinction in one step from very high values above K is about $\exp(-K)$.

For the Ricker case (and the Hassell with $b > 1$) the situation is different.

Proposition. Let K be a (large) positive number, let L be a given random variable and let KL_t be an i.i.d. sequence. If the support of the random variable L is all of $(0, \infty)$ with a heavy tail then the expected life-time of the branching process following the Ricker model grows slower than exponentially in K.

If pure growth is allowed with positive probability ($L = \infty$) then the expected life-time is polynomial.

Proof sketch.

First take an $m, 0 < m < \exp r$ and identify a point x^* such that $\exp(r - x) > m$ for $0 < x < x^*$. Take a fixed K and let the random carrying capacity sequence be KL_t. Put $\mathbf{P}\{L < 1\} = q$.

Then choose a large G such that the extinction probability of the process given that $Z_t > G$ and $L_{t+1} < 1$ is at least $1/2$.

G may be chosen to be $2K \log K$ asymptotically: The extinction probability from level G is about $(1 - \exp(-\frac{G}{KL_{t+1}}))^G$ which is larger than $(1 - \exp(-2 \log K))^{2K \log K}$ which is turn tends to 1 for large K.

Now we notice that a long sequence of "good years" with KL large enough will take the process to the level G.

If $L > \frac{2 \log K}{x^*}$ then the process grows at the rate m with probability at least $\frac{1}{2}$ until the level $2K \log L$ is reached.

It takes at most $n_K = \frac{\log G}{m}$ steps to reach the level G. At this level the probability of immediate extinction is at least $\frac{q}{2}$.

Now the probability of extinction in at most $n_K + 1$ steps is

$$\frac{q}{2} p_K^{n_K}$$

where $2p_K$ is the probability of $L > \frac{2 \log K}{x^*}$.

If the exit time is denoted by T then we get that

$$\mathbf{E}T \leq \frac{2}{q}(n_K + 1)p_K^{-n_K}.$$

Let us for a moment let p be constant (as it is in the case with unlimited growth) then the expression

$p^{-n_K} = \exp(-\frac{\log(2K \log K)}{m} \log p)$ which is less than

$$K^{\frac{3}{2m} \log \frac{1}{p}}$$

asymptotically.

If L has an exponential tail we get that p_K is of the form $\exp(-c \log K)$ for some positive c. The whole expression for $\mathbf{E}T$ is then majorized by

$$K^{\frac{3}{2m} c \log K}$$

disregarding some factors of less importance.

If L has a heavier tail we get a slightly slower growth of $\mathbf{E}T$.

Remark. In the Hassell case the point G is of the form K^a where the exponent a should be taken larger than $\frac{b}{b-1}$. If L has exponential tails we would get

$$\mathbf{E}T \leq K^{\frac{a}{m} c K^{a-1}}.$$

Finally, we see that sudden extreme shocks effectively reduces the expected life-time drastically.

The setup is the same as in the preceding discussion. K is fixed and the random carrying capacity is KL_t where L has a given distribution on the whole of $(0, \infty)$. We assume further that it has a density $c > 0$ at 0 and that its mean is 1.

Proposition. The expected extinction time for the size-dependent branching process generated using the Beverton-Holt model is linear in K.

In the Hassell case it is of the order of $K^{\frac{1}{b}}$ and for the Ricker model a constant times $\log K$.

Proof idea.

Take the Beverton-Holt case first. We suppose that the process has attained the level $Z_t = K$. Then a carrying capacity of KL_{t+1} will kill the process with probability (dropping the subscripts for simplicity)

$$(1 - \frac{1}{1 + \frac{K}{KL}})^K$$

which is about $\exp(-KL)$. Thus if $KL = 1$ the probability is e^{-1}.

$\mathbf{P}\{L < \frac{1}{K}\}$ is approximately $\frac{c}{K}$. Then we have a probability of $\frac{c}{Ke}$ of immediate extinction from level K.

The expected time of extinction $\mathbf{E}T$ will then be at most $\frac{Ke}{c}$. (The time of attaining level K or below is tacitly assumed to be small.)

For the Ricker model (assuming the level rK) the same kind of argument gives us

$$\mathbf{E}T \leq \frac{e \log rK}{c}.$$

In the Hassell case we get a life-time of the order of $K^{\frac{1}{b}}$.

Remark. If we dispense with the assumption that we have a positive density at 0, a much more refined analysis of the probability of small L (or big $\frac{1}{L}$) is needed.

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