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Published in:
Stochastic Models

DOI:
10.1080/15326349.2019.1578241

Published: 01/01/2019

Document Version
Accepted author manuscript

On the lifetime of a size-dependent branching process

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Keywords: Branching processes, quasi-stationary distribution, large deviations, random environment, growth-catastrophe behavior

AMS: 60J80, 60J05, 60J20,60F10,92D25

Abstract

We discuss lifetimes for a family of population-dependent branching processes. The attenuation factor (due to environment or competition, for example) is of Ricker type, i. e., the probability of an individual having offspring at all is of the form $e^{-\gamma n}$ if the total population is n. Equivalently we can write the probability as $e^{-\frac{n}{K}}$ where the *carrying capacity* K is γ^{-1}, the inverse of the attenuating factor. It is well known that the expected lifetime of such a process is exponential in K. If the carrying capacities $\{K_t\}$ vary much over time, for instance, if they are i.i.d. with a heavy-tailed distribution, the extinction scenario may change to a growth-catastrophe one with expected lifetimes much shorter. In addition to Ricker's model, production functions of the Beverton-Holt and Hassell types are also discussed.

1 Introduction

In this study we will look at some simple size-dependent branching processes with varying carrying capacities. The shape of the (deterministic) production function is decisive when it comes to certain modes of extinction, in particular the growth-catastrophe behavior. A *production function* or *stock-recruitment* function of a discrete-time population model expresses the number of individuals in the next generation as a function of the present number of individuals. Alternatively, it expresses the density of the next generation as a function of the present density.

The productions functions studied are of the Beverton-Holt, Hassell, and Ricker type, respectively:

(Beverton-Holt)

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

(Hassell)

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

(Ricker)

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

where z is the population size, K the carrying capacity[1] , $r > 1$ or $e^r > 1$ the mean growth rate at small sizes, $b \geq 1$ is a parameter. We notice that the Beverton-Holt model is increasing as a function of z, while the Hassell model (with $b > 1$) is eventually decreasing. The Ricker function approaches 0 very fast for large z meaning that large over-population may reduce the next generation dramatically.

It is well known that most size-dependent branching models have a lifetime whose expectation is exponential in the carrying capacity K, [4]. A study by Hamza, Jagers and Klebaner [3] exhibits an explicit expression for the dependence in a simple, but

[1]Here K does not play the role of a "carrying capacity" in the sense that, in general, it is not the threshold value separating population short-term growth and decline. Rather, the fixed point of the production function is the value at which the next generation is equal to the present one. The fixed points are, respectively, $(r-1)K, (r^{\frac{1}{b}}-1)K, rK$.

illustrative case. One of the conclusions drawn is that extinction rarely depends on demographic variation in a fixed environmental setting: the lifetime is usually extremely long, compare Figure 1 below. Previous studies, such as [5], suggest that fluctuating environment (fluctuating carrying capacity) may shorten the lifetime considerably. In particular, such behavior is to be expected when extreme fluctuations have a comparatively high probability. On the other hand, if the carrying capacities vary independently within a bounded interval, the study in [5] suggests that the lifetime behaves roughly as in the constant carrying capacity case. The main focus in this paper will be, then, on the case with fluctuating environment, as in Figures 2 and 3 below.

The size-dependent branching models $\{Z_t\}$ are constructed as follows. Take an offspring distribution q, the *nominal* offspring distribution, with mean r (e^r in the Ricker case) and variance σ^2. Let the number of individuals at time t (or in generation t) be Z_t and define for $t = 0, 1, 2, \ldots$

$$Z_{t+1} = \sum_{j=1}^{Z_t} \xi_{j,t} \quad \text{if} \quad Z_t > 0,$$

and $Z_{t+1} = 0 \quad \text{if} \quad Z_t = 0$, where the offspring $\xi_{j,t}, j = 0, 1, 2, \ldots Z_t$ are i.i.d. random variables.

In the general formulation of our process, the carrying capacities $\{K_t\}$ are taken to be a sequence of i.i.d. random variables. Most importantly, K_t is assumed independent of $Z_0, Z_1, \ldots Z_{t-1}$. Given a carrying capacity K_{t+1} the individuals of generation t produce offspring, independently of each other, with probability

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

in the Beverton-Holt, Hassell, and Ricker cases, respectively. If an individual produces offspring, the number of descendants follows the nominal offspring distribution q. Thus we obtain, in the Ricker model, $\mathbf{P}\{\xi_{j,t} = k | Z_t, K_{t+1}\} = \exp(-\frac{Z_t}{K_{t+1}})q_k, k = 1, 2, \ldots$. Under the same conditions, the conditional probability of $\xi_{j,t}$ being 0 is $1 - \exp(-\frac{Z_t}{K_{t+1}})(1 - q_0)$ and the conditional probability of $Z_{t+1} = 0$ (extinction) is $(1 - \exp(-\frac{Z_t}{K_{t+1}})(1 - q_0))^{Z_t}$. For the Beverton-Holt and Hassell models the conditional distributions are calculated in an analogous way. If $K_t = K$ for all t we are, of course, in the constant carrying capacity situation.

The conditional means follow the production functions closely. $\mathbf{E}\{Z_{t+1} | Z_t, K_{t+1}\}$ are in the three cases

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

respectively.

The process $\{Z_t\}$ is a Markov chain on the set of non-negative integers Z_+ or on some sublattice dZ_+. The binary example in Section 2 lives on $2Z_+$, the even non-negative integers. In either case, the Markov chain is irreducible on its state space. If the carrying capacity is large and constant the process follows the corresponding deterministic dynamical system in the short run, [8, 4]. Technically, this is due to the fact that when Z_t is large the standard deviation of Z_{t+1} is small compared to its mean. Depending on the behavior of the deterministic system our process may, for some time, look convergent, periodic or chaotic as the case may be. However, in the long run the chain is always aperiodic and it goes extinct (reaches the absorbing state 0) eventually. The chain admits a quasi-stationary distribution and the time to absorption is exponential in K, [3, 4].

Let us look at a few illustrative examples. In Figure 1 we see a portion of a simulated trajectory of a size-dependent Ricker-type branching process $\{Z_t\}$ with constant carrying capacity $K = 30$. The nominal offspring distribution has mean 2 so the equilibrium size is $K \log 2 \approx 20.8$. The lifetime of this particular trajectory is 6228. The average lifetime of 10000 simulations was 23724.6. In Figure 2 the carrying capacities are i.i.d. with a heavy-tailed distribution with a median of 30. The trajectory has a lifetime of 861. The average lifetime of 100000 simulations was 195.6. In Figure 3 the setup is similar: the median carrying capacity is 500. In this case the average of 100 simulations was 9371.4. In Figures 2 and 3 it is noteworthy that the extinction mechanism seems to be extraordinary growth followed by immediate extinction, a so-called *growth-catastrophe* behavior. Of course, other extinction mechanisms are possible as well.

The paper is organized as follows. In Sections 2 and 3 we do some preparatory work to motivate the quantitative results in Section 4. In Section 2 we briefly review a simple concrete example with a binary branching mechanism. It is one of the rare instances where we can find an explicit quantification of the lifetime. In Section 3 we look at how the branching processes with different production functions react to dramatic changes in carrying capacity. More precisely, we investigate the probability of extinction when the carrying capacity suddenly drops. The calculations suggest that for the Ricker and Hassell models excessive growth may result in subsequent extinction, while the Beverton-Holt model survives growth more easily. In the final Section 4 we prove quantitative estimates for the growth of the lifetimes in terms of the carrying capacities. The calculations are based on a growth-catastrophe mechanism of extinction, i. e., the process grows very much during a run of advantageous time periods (years) followed by extinction when a "bad" or "ordinary" year follows. As far as we can tell the quantitative results in Proposition 1 are new.

2 The Binary Example

In the size-dependent discrete-time branching process studied in [3] we have Z_t individuals or particles at time $t, t = 0, 1, \ldots$. At time $t+1$ each individual, independently of the others, gives birth to two offspring and dies with probability $\frac{K}{K+Z_t}$, or dies with no offspring with complementary probability. In other words, we are looking at a Beverton-Holt-type size-dependent branching process with a one-point nominal offspring distribution, $q_2 = 1$.

The mean of the process at time $t+1$, given that we have Z_t individuals 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 K, the attracting fixed point of the corresponding deterministic map. The time of descending below the level $\frac{K}{2}$ has an 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 [6], compare also [10]. The process close to K may also be approximated by a linear autoregressive process [8]. The exit time for the autoregressive process is even longer, it is of the order of $\exp(\frac{3}{32}K)$, [7, 9].

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

While fixed K is all our cases always lead to lifetimes 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 Rickel model be 4, say. The deterministic model is chaotic; the quotient between the largest and smallest value in a typical trajectory is in the millions. More exactly, it is e^{e^3-4}. The probability of immediate extinction from a large level, such as $20K$ is about

$$(1 - \exp(-20))^{20K} \approx 1 - 20K\exp(-20)$$

for moderate K.

3 Resilience to Sudden Shocks

Let us now assume that the carrying capacities are time-dependent: K_t, $0 \leq t < \infty$, form an i.i.d. sequence of random variables on the whole positive real line $(0, \infty)$. The real-valued process on $(0, \infty)$ obtained by iteration of a sequence of production functions with these random carrying capacities is then positive recurrent [2] (under some mild conditions). This suggests that the process spends much time where the bulk of the invariant distribution lies. Intuitively, we would expect our branching processes to be frequently, at least initially, within an order of magnitude from the mean or median carrying capacity.

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

Given the sequence of carrying capacities the conditional probabilities of immediate extinction $\mathbf{P}\{Z_{t+1}=0|Z_t,K_{t+1}\}$ are in the three models

$$(1-(1-q_0)\frac{1}{1+\frac{Z_t}{K_{t+1}}})^{Z_t}, \quad (1-(1-q_0)\frac{1}{(1+\frac{Z_t}{K_{t+1}})^b})^{Z_t}, \quad (1-(1-q_0)\exp(-\frac{Z_t}{K_{t+1}}))^{Z_t},$$

respectively.

If we assume that the carrying capacity has been fairly constant for some time so Z_t lies in the vicinity of its equilibrium point and that K_{t+1} is only a tenth of the previous value, then we have, in the Beverton-Holt case, a small probability of immediate extinction, it is only about $(1-(1-q_0)/11)^{K_t}$ which is less than $\exp(-\frac{(1-q_0)K_t}{11})$. For $r=2, q_0=.02$ it is .393 (.0094) when $K_t=10\ \ (50)$.

In a similar scenario for the Hassell models with $b>1$ and Z_t at its equilibrium level $(r^{\frac{1}{b}}-1)K_t$ extinction is probable for small K_t: For $b=3, r=2, q_0=0.02$ and $K_t=10\ \ (50,100)$ it is .946 (.758, .576).

In the Ricker case we assume that Z_t lies close to the equilibrium level rK_t. Here the probability of immediate extinction is appreciable for moderately large K_t, it is of the order of $(1-(1-q_0)e^{-10r})^{rK_t}$. The value is about .993 (.936, .515) for $r=\log 2, q_0=.02$ and $K_t=10\ \ (100,1000)$.

4 The Growth-Catastrophe Scenario

The nature of these one-dimensional models is such that, if the process survives a sudden drop in carrying capacity, it adapts to this change in the environment immediately. Several "equally bad years" in a row are roughly speaking no worse than the first shock. On the other hand, we saw above that overpopulation is a threat in the Hassell and Ricker cases: the discrete-time model may not be able to limit excessive growth (as opposed to models in continuous time) until it is too late. A sequence of good years is likely to result in excessive growth. A low carrying capacity during the following year may lead to exctinction. This is the so-called growth-catastrophe scenario. We will now see that extinction through excessive growth followed by a catastrophe may in some cases lead to shorter than exponential lifetimes.

We saw above that 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 one with $b >> 1$) the situation is different, however.

We will express the lifetimes of our processes in terms of the *level* K of the i.i.d. sequence of carrying capacities. For example, K could be the median carrying capacity. To be more precise, let the random carrying capacity sequence be of the form $\{KL_t\}$ where $\{L_t\}_{t\geq 1}$ is a given i.i.d. sequence. The random variable L_t may be heavy-tailed; let us assume that its median is 1.

Proposition 1. *Let K be a (large) positive number and let $\{KL_t\}_{t\geq 1}$ be an i.i.d. sequence of carrying capacities. If the support of the random variable L_t is an unbounded interval of the form $(A, \infty), 0 < A < 1$, and its distribution has a heavy tail* *then the expected lifetime of the branching process following the Ricker model grows slower than exponentially in K.*

If pure growth is allowed with positive probability, i.e., L can take the value ∞ (or, equivalently, there is no attenuating factor) with positive probability, then the expected lifetime grows polynomially in K.

The same conclusions hold for the branching process following the Hassell model with $b >> 1$.

Proof.

Let G be a large positive integer, to be defined below. The idea of the proof is that a long sequence of "good years" with large enough carrying capacity will take the process with a high probability from 1 (or any other level below G) in a small number of steps to the level G.

Let the random carrying capacity sequence be KL_t. Denote $\mathbf{P}\{L < 1\}$ by ρ. $0 < \rho \leq \frac{1}{2}$ since L is supported on (A, ∞) and its median is 1. Choose G large enough so that the extinction probability in one step 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 $(1 - \exp(-\frac{G}{KL_{t+1}})(1 - q_0))^G$ which is about $(1 - \exp(-2 \log K))^{2K \log K}$ which in turn tends to 1 for large K. We will now calculate the number of favorable years (steps) needed to reach the level G with high probability.

First take an m, $1 < m < e^r$, and identify a point x^* such that $e^r > \exp(r - x) > m$ for $0 < x < x^*$. If $L > \frac{2 \log K}{x^*}$ then the Ricker modification of the binary process described in Section 2 grows at a rate greater than m with probability at least $\frac{1}{4}$ until the level $G = 2K \log K$ is reached: The probability of a binomial process exceeding its mean is at least $\frac{1}{4}$, [1], and in our situation the conditional mean of Z_{t+1} given $Z_t < G$ and $L_{t+1} > \frac{2\log K}{x^*}$ is $Z_t \exp(r - \frac{Z_t}{KL_{t+1}})$ which is larger than $Z_t \exp(r - x^*) \geq mZ_t$. The number of steps needed to reach G is at most (the smallest integer exceeding) $\frac{\log G}{\log m}$ and the probability of such a scenario followed by extinction in the next step is at least

$$(\frac{p_K}{4})^{n_K} \cdot \frac{\rho}{2},$$

where $n_K = \lceil \frac{\log G}{\log m} \rceil$ and $p_K = \mathbf{P}\{L > \frac{2\log K}{x^*}\}$.

If the time of extinction is denoted by T then we get that

$$\mathbf{P}\{T > n_K + 1\} \leq 1 - \frac{\rho}{2}(\frac{p_K}{4})^{n_K}$$

whence

$$\mathbf{E}T = \sum_{i>0} \mathbf{P}\{T > i\} \leq \sum_{i>0} (n_K + 1)(1 - \frac{\rho}{2}(\frac{p_K}{4})^{n_K})^i = (n_K + 1)\frac{2}{\rho}(\frac{p_K}{4})^{-n_K}.$$

In the general case we may argue as follows. The one-step conditional variance given Z_t and KL_{t+1} is of the same order of magnitude as its mean, [4]: the conditional mean is $Z_t \exp(r - \frac{Z_t}{KL_{t+1}})$ and the conditional variance $Z_t \exp(-\frac{Z_t}{KL_{t+1}})(\sigma^2 + e^{2r} - e^{(2r - \frac{Z_t}{KL_{t+1}})}) < Z_t(\sigma^2 + e^{2r})$. Recall that σ^2 is the variance of the nominal offspring distribution. Given that $KL_{t+1} > \frac{G}{x^*}$, by the Chebyshev Inequality the conditional probability of Z_{t+1} exceeding $\frac{1+m}{2}Z_t$ is at least $\frac{1}{4}$ for Z_t larger than some level z^*, essentially depending only on the offspring distribution of the process: $\sqrt{z^*} > 2\sqrt{\frac{4}{3}}\sqrt{\sigma^2 + e^{2r}}/(m-1)$. In particular, z^* does not depend on K. Denote $(1+m)/2$ by $m' > 1$. If the growth rate of the process is at least m' it takes at most $n'_K \equiv \lceil \frac{\log G}{\log m'} \rceil$ steps to reach the level G from level z^*. The probability of this event followed by extinction in the next step is at least $(\frac{p_K}{4})^{n'_K+1}\frac{\rho}{2}$

Starting from the level one there is a large conditional probability that z^* is reached in at most $n' \equiv \lceil \log z^*/\log 2 \rceil$ steps. To see this, note that the probability of an individual giving rise to two or more descendants is at least $(1-q_0-q_1)e^{-\frac{z^*}{KL_{t+1}}}$ as long as the total population Z_t lies below z^*. Under the condition $L_{t+1} > \frac{2\log K}{x^*}$ this probability is $> (1-q_0-q_1)me^{-r}$. Hence the conditional probability of reaching z^* from 1 in at most n' steps is at least $((1-q_0-q_1)me^{-r})^{n'}$. As the last expression is independent of K we may call it C for simplicity.

Thus the probability of extinction in at most $n'_K + n' + 1$ steps is at least

$$C\frac{\rho}{2}(\frac{p_K}{4})^{n'_K}p_K^{n'} > C\frac{\rho}{2}(\frac{p_K}{4})^{n'_K+n'}$$

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

If the time of extinction is denoted by T then we get that

$$\mathbf{P}\{T > n'_K + n' + 1\} \le 1 - C\frac{\rho}{2}(\frac{p_K}{4})^{n'_K+n'}$$

whence

$$\begin{aligned}\mathbf{E}T = \sum_{i>0}\mathbf{P}\{T > i\} &\le \sum_{i>0}(n'_K + n' + 1)(1 - C\frac{\rho}{2}(\frac{p_K}{4})^{n'_K+n'})^i \\ &= (n'_K + n' + 1)\frac{2}{C\rho}(\frac{p_K}{4})^{-n'_K-n'}.\end{aligned}$$

We note that this formula has the same form as the (slightly) simpler formula derived above for the binary process.

Let us for a moment consider the case of p constant > 0 (as it is when we may have unlimited growth, meaning that there is no attenuating factor, with positive probability). Then the expression

$$(\frac{p}{4})^{-n'_K - n'} = \exp((n'_K + n') \log \frac{4}{p}) \leq \exp((\frac{\log(2K \log K)}{\log m'} + n') \log \frac{4}{p}) \approx (2K \log K)^{\frac{\log \frac{4}{p}}{\log m'}}$$

asymptotically. In other words, the growth is polynomial in K.

If the distribution of L has an exponential tail we get that p_K (as well as $\frac{p_K}{4}$) is of the order of $\exp(-c \log K)$ for some positive c. The whole expression for $\mathbf{E}T$ is then majorized by

$$(2K \log K)^{\frac{c}{\log m'} \log K}$$

disregarding some factors of less importance. Thus the growth of $\mathbf{E}T$ is clearly subexponential as a function of K. On the other hand, the above expression grows faster than polynomially.

If L has a heavier tail we get a still slower growth of $\mathbf{E}T$. For example, if the tail is polynomial so that p_K is of the form $c(\log K)^{-d}$ for some $c, d > 0$, then $\mathbf{E}T$ is majorized by an expression of the order of

$$(2K \log K)^{\frac{d \log \log K}{\log m'}}.$$

In the Hassell case, with a parameter $b >> 1$, we can proceed in complete analogy with the above. The point G may be taken to be of the form K^a where the exponent a should be larger than $\frac{b}{b-1}$. Take $m \in (1, r)$ and choose x^* so that $r > \frac{r}{(1+x)^b} > m$ for $0 < x < x^*$. Given Z_t and KL_{t+1} the conditional variance of Z_{t+1} is less than

$Z_t \frac{1}{(1+\frac{Z_t}{KL_{t+1}})^b}(\sigma^2 + r^2)$, so we can use the same Chebyshev Inequality argument as above to find a suitable z^* such that for the process in the interval from z^* to G the conditional probability of larger growth than $m' = (m+1)/2$ is more than $\frac{1}{4}$. The number n'^K of such steps to G is less than $\lceil \frac{a \log K}{\log m'} \rceil$. Again, the conditional probability of the process going from 1 to z^* in $\frac{\log z^*}{\log 2}$ steps is (minorized by an expression) independent of K.

In the case where L has an exponential tail $\frac{p_K}{4}$ is of the form $\exp(-cK^{a-1})$ and so

$$\mathbf{E}T \leq K^{\frac{a}{\log m'} cK^{a-1}}.$$

Since a can be chosen slightly larger than $\frac{b}{b-1}$, $a - 1 \approx \frac{1}{b-1}$. Thus for $b > 2$ we can take $a - 1 < 1$ so the expression grows subexponentially as a function of K.

The corresponding calculation for polynomial tail yields

$$\mathbf{E}T \leq K^{d(a-1) \log K \frac{a}{\log m'} \log K}.$$

Remark. The study above pertains to carrying capacities of the same order of magnitude as K (or larger). What can be expected from very *small* carrying capacities, L taking values close to 0? It seems that the process goes extinct via one catastrophic drop in carrying capacity, which has much higher probability than the growth-catastrophe scenario.

We saw in Section 3 that immediate extinction from a level Z_t has probability $(1 - (1-q_0)\exp(\frac{-Z_t}{KL_{t+1}}))^{Z_t}$ (in the Ricker case). For examle, if $\log L$ has exponential left tails, with parameter λ, and Z_t is at level rK, this probability is at least

$$e^{-(1-q_0)}(\frac{\log(rK)}{r})^{-\lambda}.$$

If L has finite expectation the corresponding continuous state space process on the positive real line is positive recurrent, [2]. That process returns to the neighborhood of rK (which is usually close to the center of the invariant probability distribution of the process) fast from low values. So assuming the same kind of behavior for our branching process, i. e., return to level rK is fast (in about $\log rK$ steps) from low values (almost extinction), the expected lifetime is seen to be effectively majorized by the reciprocal of the above expression:

$$\mathbf{E}T = O((\log rK)^{\lambda}).$$

Under the same assumptions for L, the corresponding immediate extinction probability for the Beverton-Holt model from level K is of the order of $e^{-(1-q_0)}(K-1)^{-\lambda}$ and thus the lifetime would be of the order of K^{λ}.

Acknowledgements: The research was supported by a grant from the Magnus Ehrnrooth Foundation. Thanks are due to the organizers of WBPA18 for a most agreeable and fruitful workshop. I would also like to thank Sophie Hautphenne, Fima Klebaner and Vladimir Vatutin for interesting discussions and references. I thank the referee for many valuable suggestions how to improve the paper.

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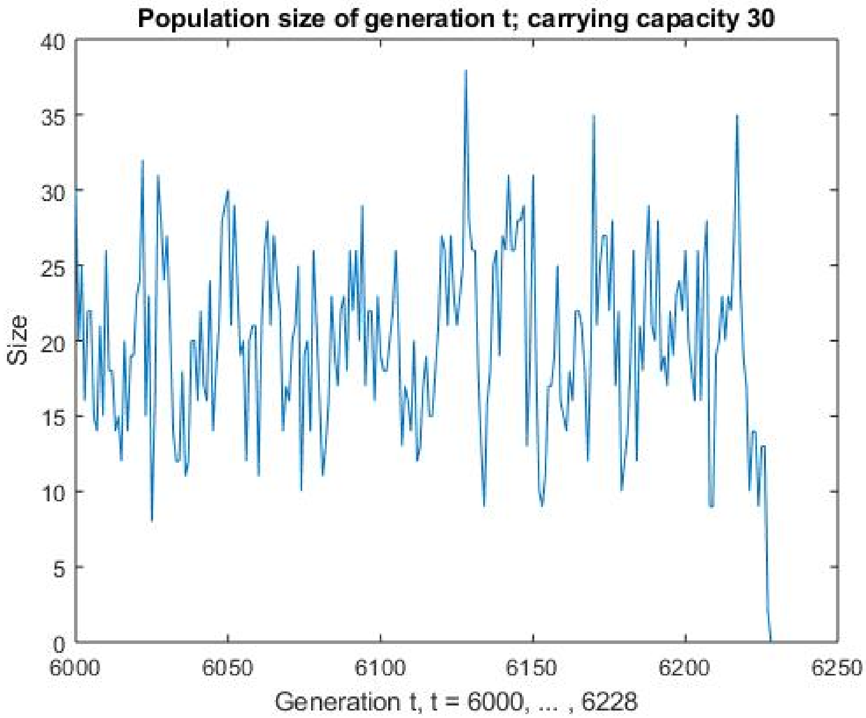

Figure 1: Simulated trajectory of a Ricker-type size-dependent branching process $Z_t, t = 6000, \dots 6228$, where the carrying capacity $K = 30$, the nominal offspring distribution has mean $e^r = 2$ and variance $\sigma^2 = 1.2$. The corresponding deterministic Ricker function $z \to z \exp(r - \frac{z}{K})$ has a fixed point at $rK \approx 20.8$.

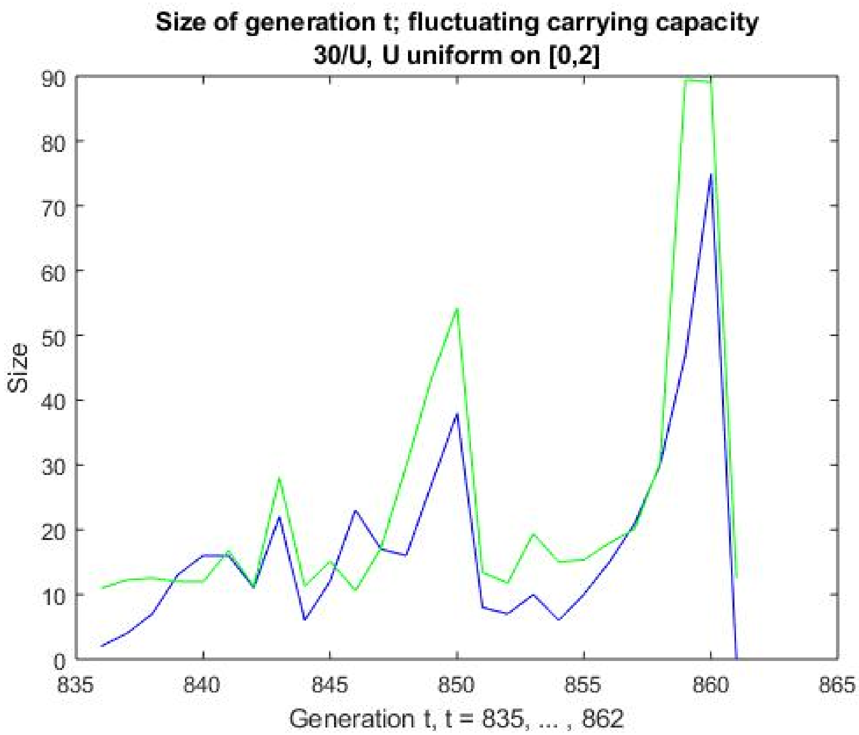

Figure 2: Simulated trajectory of a Ricker-type size-dependent branching process $Z_t, t = 835, \ldots 862$, (blue curve) where the carrying capacity $\{KL_t\}$ is an i.i.d. sequence with the distribution $30/U$ where U is uniform on [0,2]. The superimposed green curve is $\{rKL_t\}, t = 835, \ldots 862$ corresponding to the equilibrium points of the random Ricker production functions. The nominal offspring distribution has mean $e^r = 2$ (thus $r = \log 2$) and variance $\sigma^2 = 1.2$.

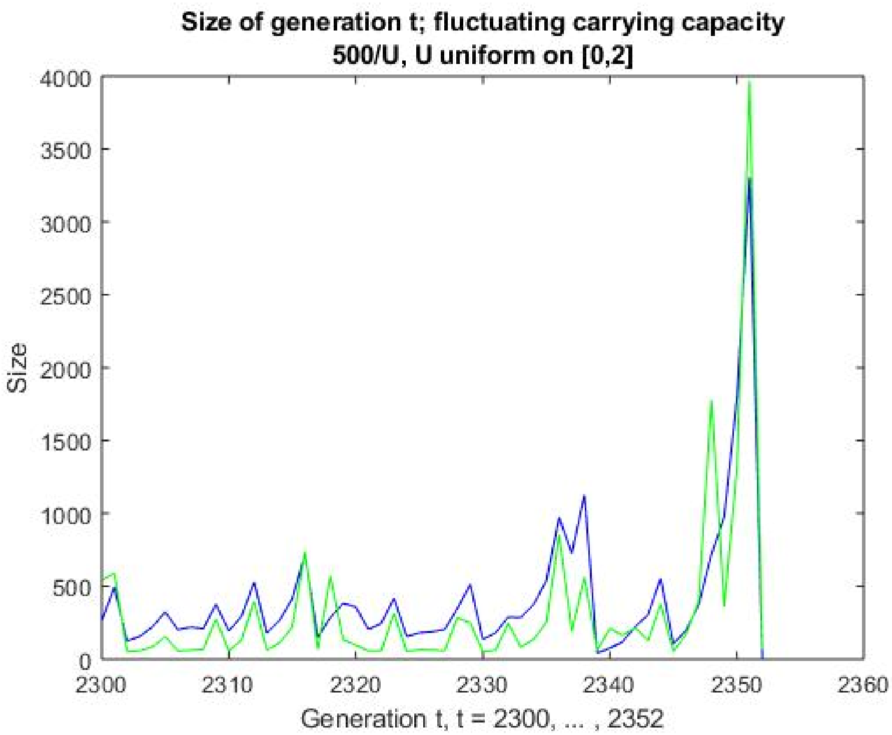

Figure 3: Simulated trajectory of a Ricker-type size-dependent branching process $Z_t, t = 2300, \ldots 2352$, (blue curve) where the carrying capacity $\{KL_t\}$ is an i.i.d. sequence with the distribution $500/U$ where U is uniform on [0,2]. The nominal offspring distribution has mean $e^r = 2$ and variance $\sigma^2 = 1.2$. The superimposed green curve is $\{KL_t/5\}$ for the same t-values; it is normed to fit into the same display.