

Structure Dependent Branching Processes - problems and ideas.

Peter Jagers

(Joint work with F. C. Klebaner et al.)

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Classical branching processes - delightful mathematics. But as population biology?

1. No sex – (In branching processes) a woman needs a man like a fish needs a bicycle (Irina Dunn, Australian Parliament Senator).
2. No limitations, no competition; extinction or exponential growth for ever!
(1) – Our hosts' showpiece, but little for general processes in continuous time. (2) – Attempts from us and others: population size dependence.

First: (2) Population size- and age-dependent processes

- Birth during life, and/or split at death, after a life span with an arbitrary distribution, all dependent upon individual age and population size:
- The birth intensity of an a -aged individual in a population of size z is $b_z(a)$ and the death rate similarly $h_z(a)$.
- At death children may also be produced. The distribution of their number $\{p_z(a)_k; k=0,1,2,3, \dots\}$ may depend on mother's age a at death and on the age and on the size z then.
- Denote the population size at t by Z_t , and the whole vector of ages by A_t , so that $Z_t = |A_t|$.

Population Feedback Loop: Individual reproduction \rightarrow population change \rightarrow environment \rightarrow individual reproduction.

- Some (most?) populations exhaust their environment, and can't persist. But what about those who don't and live sustainably?
- Still their **habitat** has a **Carrying Capacity** K : small populations are supercritical but reproduction turns subcritical whenever population size $Z_t > K$. Sustainability means that K is not eroded but remains constant.

What about such populations, starting from a little Z_0 (think: 1)?

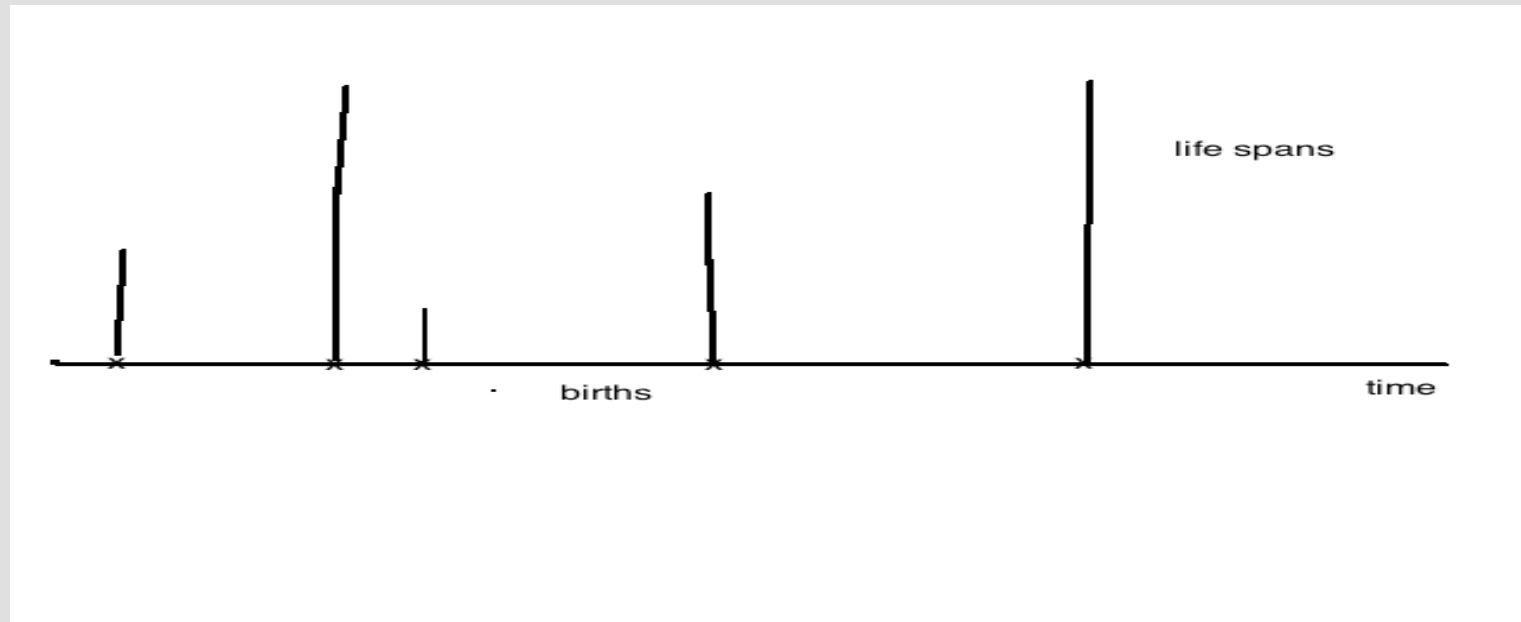
- Extinction or invasion?
- Growth phase up to around K – exponential?
- Persistence for ever? – No way.
- The duration of the plateau phase, in between the growth stage and that of decline into ultimate extinction for K large – more difficult.
- The behaviour during the time around K – stabilising age distributions, as $K \rightarrow \infty$?
- Extinction phase – what do the path and time to ultimate extinction look like?

The initial stage: Extinction or Invasion

- One basic assumption, monotonicity in viability: if $\{Y_t\}$ is a not population size dependent process with parameters frozen at $z \leq Z_u$, $u \leq t$, and $Z_0=Y_0$, then $Y_t \geq Z_t$ in distribution. The converse holds, if $z \geq Z_u$. And a simple remark:
- If $T_a = \inf \{ t; Z_t \geq aK \}$, then $Z_t \geq Y_t$ on $\{T_a \geq t\}$, where $\{Y_t\}$ is the process with parameters frozen at aK and $Y_0 = Z_0 = z < aK$.
- Write T = time to extinction.
- $P_K(\text{early extinction}) = P(T < T_a) = P(\sup Z_t < aK) \leq P(\sup Y_t < aK) = P(Y_t \rightarrow 0) = q(aK)^z$, if $q(y)$ denotes the classical extinction probability of the process with parameters frozen at population size y .

But can't we do better?

- Using ideas from epidemic processes (Ball, Barbour, cf. the next talk!) we can couple the population-size-dependent process to an ordinary branching process, starting the same and with the parameters frozen, as long as $Z_t = o(\sqrt{K})$ ($= O(K^{2/3})$?).
- Argument: keep the successive birth points of the branching process with probabilities = ratios of the relevant birth intensities. Regard life spans as marks of the points, converging as $K \rightarrow \infty$.
- Hence, $q(aK)^z \geq P_K(\text{early extinction} | Z_0=z) \rightarrow q(z)^z$.
- Hope: the first step of a unified description of the whole population life cycle.



Keep a birth at time t with probability

$b_{z(t)}^K(a_t^{\text{mother}}) / b_{z(0)}^K(a_t^{\text{mother}})$. Take the infimum $\gamma(xK, K)$ over ages and study

$\gamma(xK, K)^{z(\tau(K))}$, where $x(t)K = z(t)$, and $\tau(K)$ is

a time point chosen so that this $\rightarrow 1$, as $K \rightarrow \infty$.

Growth

- If a branching process does not die out, it grows exponentially:
- Hence, $aK \approx Z_{T_a} \geq Y_{T_a} \approx We^{\alpha(aK)T(a)}$, W a non-negative r.v. with $E[W] = z$, $\alpha(aK)$ is the Malthusian parameter of the $\{Y_t\}$ -process and $T(a) = T_a < \infty$.
- In other words, $T_a = O(\log K)$, if it is finite.

The (Quasi-)Stationary Phase

- Once in the vicinity of K , population size should linger there for a time that is exponential in K , as $K \rightarrow \infty$, by large deviation theory.
- Under technical assumptions we proved:
- Assume $Z_0/K \rightarrow 1$ in probability, as $K \rightarrow \infty$. Then $Z_t/K \rightarrow 1$, uniformly in probability on any bounded t -interval, as $K \rightarrow \infty$.
- Assume $Z_0/K = 1$. Write $\tau^K = \inf\{t; |Z_t/K - 1| > \epsilon\}$. Then, for some $C, c > 0$, $E[\tau^K] > Ce^{cK}$, FK & PJ in JAP 2011.
Stronger results for some discrete time, binary splitting processes (Klebaner, Sagitov, Vatutin, Haccou, and PJ.)

What happens during the pseudo-stable stage?

- Assume h^k, b^k, m^k all bounded and Lipschitz, in the sense that
- $|h_z^k(a) - h_y^k(a)| \leq C|z-y|/K,$
- and that the initial age distribution A_0^k/K has bounded total mass and converges weakly to some A_0^∞ , as $K \rightarrow \infty$. Then,
- The age distribution process $\{A_t^k/K; t \geq 0\}$ is tight and converges weakly, as $K \rightarrow \infty$, in Skorohod space $D(\mathbb{R}_+, M(\mathbb{R}_+))$, to a non-random limit, describable by the classical McKendrick-von Foerster equation for its density,
- $(\partial_t + \partial_u)a(t, u) = -a(t, u)h_{z(t)}.$
- What about the type distribution?

The Time of Descent

- Thus, finally any band around K will be left, never to be returned to.
- So, how long, T_d , does it take from then until extinction?
- For classical, general subcritical branching processes starting from aK , the time to extinction is $O(\log K)$ (PJ, Klebaner, and Sagitov: On the Path to Extinction, PNAS, 2007).
- By a comparison argument the corresponding is true here: $E[T_d | \text{no return to } bK, b < 1] = O(\log K)$, if start from aK , $0 < a < b$. (J. Math. Biol. 2016)

General Branching with Structure Dependence

- It's now merely a matter of notation to generalise, having individual life dependent not only on population size and but also upon composition:
- If the age structure is $A=(a_1, a_2, \dots, a_z)$, the birth rate of an a -aged individual is $b_A(a)$ and the death rate similarly $h_A(a)$.
- At death children may also be produced. The distribution $\{p_A(a)\}$ may depend on mother's age a at death and on the age configuration A then.

But what is criticality in an age-structured population?

- (Super/sub)critical, as $Z_t \rightarrow K$. Frozenly? Independently of ages?
- Introduce a criticality function:

$$\chi_A = b_A + h_A(m_A - 1),$$

And the generating function ϕ_A of the number of children at splitting. To prove exponential holding time we used:

- Births during mother's life occur one by one.
- $|\chi_A| \leq C ||A|/K - 1|$ (Lipschitz at K) and
- $(e^{1/K} - 1)b_z + (\phi_z(1/K) e^{-1/K} - 1)h_z \leq 0$ for $z > CK$ (subcriticality at overcrowding)

Strict criticality

- The Lipschitz condition implies **strict criticality**,
- $\chi_A = 0$, if $|A|=K$. OK for Bellman-Harris and b.a.d. processes. But not in general, where child bearing and death occurs at different ages.
- Maybe we can try **Lipschitz in composition**,
 $|(\chi_A, A)/K| \leq C ||A|/K - 1|$, for $A/K \rightarrow A_\infty$?
- $(f, A) = \int f dA$.

High time for sex!

- At the cost of more burdensome notation, the preceding formulation extends to age- and type-structure dependent reproduction, $S = (a_1, t_1, a_2, t_2, \dots, a_z, t_z)$, the s -birth rate of a t -type a -aged individual is $b_s^s(a, t)$ and death rate and splitting probabilities similarly.
- We have a look at two-sex populations: $t_i = \text{♀}$ or ♂ , a new-born being female with, say, probability $1/2$, independently of everything else.

Recall: General processes are (and are not) Markov!

- If the process is single type, it is **Markovian in the age and structure**, A_t the array of ages at t , $Z_t = (1, A_t)$, $A = (a_1, t_1, \dots, a_z, t_z)$ – and correspondingly, but more burdensome, in the multi-type case:
- $L_A f = f' - h_A f + f(0)(b_A + h_A m_A)$
 - $f'(a)$ reflects linear growth in age.
 - $h_z(a)$ the risk of disappearing,
 - $b_z(a)$ the birth intensity, resulting on a 0-aged individual, and
 - $h_z(a)m_z(a)$ is the splitting intensity.
- Dynkin's formula: For $f \in C^1$,
- $(f, A_t) = (f, A_0) + \int_0^t (L_{A(s)} f, A_s) ds + M_t^f$, where $A(s) = Z_s$ and M_t^f is a local square integrable martingale.
- In particular,
- $Z_t = (1, A_t) = Z_0 + \int_0^t (b_{A(s)} + h_{A(s)}(m_{A(s)} - 1), A_s) ds + M_t^f =$
- $= Z_0 + \int_0^t (\chi_{A(s)}, A_s) ds + M_t^f$, a martingale where $(\chi_{A(t)}, A_t) = 0$, explaining the role of criticality or Lipschitz in composition.

In the two-sex case:

- $f: \{\text{♀}, \text{♂}\} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ with f boundedly differentiable in the second argument yields the f -measured population process (f, S_t) with the rate of change
- $L_S f = f' - h_S f + b_S(f(\text{♀}, 0) + f(\text{♂}, 0))/2$, where $b_S(\text{♂}, \cdot) = 0$, and there is no birth by splitting. Dynkin's formula:
- $(f, S_t) = (f, S_0) + \int_0^t (L_{S(u)} f, S_u) ds + M_t^f$, where $S(u) = S_u$ and M_t^f is a local square integrable martingale.
- In this, $f=1$, $\delta_{\text{♀}}$, or $\delta_{\text{♂}}$ yields the total population size Z_t , the number of females X_t or males, Y_t , and the birth rate of females should be dependent upon the availability of males.
- Many questions to answer, for Extremadurians and the rest of us!

Summary

- A population in a habitat that can carry a (not very) large number of individuals K , and where parameters stabilise as $K \rightarrow \infty$,
- dies out initially with a branching process determined probability,
- or else, grows to around K in time $\log K$,
- lingers there for a time $O(e^{cK})$ generations, which for $K > 10.000$ and higher organism generation times is practically infinite. In the meantime, its age and type (!) distribution stabilises.
- and then it dies out in time $\log K$.
- Maybe, by this formulation, we can approach two-sex reproduction in continuous time and age-structured populations, avoiding the difficult questions of couple formation.