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ON THE COMPLETE LIFE CAREER OF POPULATIONS IN ENVIRONMENTS WITH A FINITE CARRYING CAPACITY

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If a general branching process evolves in a habitat with a finite carrying capacity, i. e. a number such that reproduction turns subcritical as soon as population size exceeds that number, then the population may either die out quickly, or else grow up to around the carrying capacity, where it will linger for a long time, until it starts decaying exponentially to extinction.

1. Introduction

In branching processes, populations either die out or grow exponentially. Everybody in biology knows reality: If a fresh population does not die out quickly, it will enter a "log phase" of growth, after some hesitation. The expansion is followed by a so called stationary stage, which however turns into a decline period, and and ultimate extinction. Time scales may vary substantially, from short lived lab populations to long lived natural stocks.

This is certainly true for populations which exhaust the resources they are living off. Alas, as we shall see, in the very long run it also holds for populations not undermining their habitat. It suffices that there exist a *carrying capacity*, i. e. a number K such that individual reproduction is supercritical as long as the population size is smaller than K, whereas it is subcritical when the population is larger.

In discrete time branching proceses, the meaning of this is obvious: individuals beget children independently, given generation size z, and the offspring mean $m(z)$ is a decreasing function of z, $m(1) > 1$, and $m(K) = 1$. This was first analysed in a toy model of binary splitting:

$$p_2(z) = K/(K + z), \ p_0 = 1 - p_2,$$

where, as usual in simple branching processes and the like, p_k denotes the probability of an individual getting $k = 0, 1, 2, \ldots$ offspring, [5].

Here we consider general branching processes allowing birth during life, and/or split at death, after a life span with an arbitrary distribution, all dependent upon population size (and age structure), in this way: If the age structure is $A = (a_1, a_2, \ldots, a_z)$, the birth rate of an a-aged individual is $b_A(a)$ and the death rate is $h_A(a)$. For simplicity we concentrate upon population size dependence: $b_z(a), h_z(a)$. At death children may also be produced. The distribution may depend on mother's age at death and upon z. Expectation and variance of the number of children per individual are assumed bounded .

Such processes are *Markovian in the age structure*, [1], i. e. the process A_t, the array of ages at t, is Markov. We write $Z_t = (1, A_t)$, and generally, identifying points with point masses,

$$(f, A) = \int f dA = \sum_i f(a_i), A = (a_1, \ldots a_z).$$

The infinitesimal change is then described by

(1) $$L_z f := f' - h_z f + f(0)(b_z + h_z m_z).$$

where $f'(a)$ reflects linear growth in age, $h_z(a)$ the risk of disappearing, $b_z(a)$ the birth intensity, resulting in a 0-aged individual, and $h_z(a)m_z(a)$ is the splitting intensity at age a.

Dynkin's famous formula takes the form: For $f \in \mathbb{C}^1$,

$$(f, A_t) = (f, A_0) + \int_0^t (L_{Z_s} f, A_s) ds + M_t^f,$$

where M_t^f is a local square integrable martingale [2]. In particular,

(2) $$Z_t = (1, A_t) = Z_0 + \int_0^t (b_{Z_s} + h_{Z_s}(m_{Z_s} - 1), A_s) ds + M_t^1.$$

2. Growth and Criticality

By Equation 2, there is a growth trend at time t if and only if

$$(b_{Z_t} + h_{Z_t}(m_{Z_t} - 1), A_t) > 0.$$

One criticality concept is thus *criticality in the age distribution*:

$$(b_{Z_t} + h_{Z_t}(m_{Z_t} - 1), A_t) = 0,$$

giving population size a martingale character at t. A stronger concept is *strict criticality* at population size z:

$$b_z(a) + h_z(a)(m_z(a) - 1) = 0, \ a > 0.$$

Finally, a population can be called *frozen critical* at a size z if the expected number of children during a whole individual life in a population of that size is equals one.

It is natural to take processes to be monotone in the sense that if $Z_0' = Z_0$, $\{Z_t'\}$ and $\{Z_t\}$ have parameters frozen at sizes z' and z, repectively, and $z' \geq z$, then $Z_t' \leq Z_t$ in distribution. The three criticality concepts coincide for Bellman-Harris type age-dependent branching processes, where b_A vanishes and $m_A(a)$ is constant in a. Here we assume strict criticality at K. Then the process is also frozen critical there and critical in the age distribution.

Populations start small, by mutation or immigration, and thus supercritical. (This concerns clonal reproduction; the situation is somewhat different in case of sexual reproduction, where precisely small populations can easily have unbalanced sex ratios, leading to subcritical reproduction, in spite of plenty of space and resources. We shall come back to this in another connection.)

Let $0 < a < 1$. If $T_a := \inf\{t; Z_t \geq aK\}$, then $Z_t \geq Y_t$ on $\{T_a > t\}$, where $\{Y_t\}$ is a process with the same parameters frozen at aK and $Y_0 = Z_0 = z < aK$. With T denoting the time to extinction of the former process, $T := \inf\{t; Z_t = 0\}$,

$$\mathbb{P}(T < T_a) = \mathbb{P}(\sup Z_t < aK) \leq \mathbb{P}(\sup Y_t < aK) = \mathbb{P}(Y_t \to 0) = q(aK)^z,$$

where $q(y)$ denotes the classical extinction probability of the ordinary branching process with fixed parameters, viz. those frozen at population size y.

If a branching process does not die out, it grows exponentially. This applies in particular to our process $\{Y_t\}$. Hence, whenever $T_a < \infty$, and under classical conditions,

$$aK \approx Z_{T_a} \geq Y_{T_a} \approx W e^{\alpha(aK)T_a},$$

W a non-negative random variable with $\mathbb{E}[W] = z = Z_0$ and $\alpha(aK)$ is the Malthusian parameter pertaining to the branching process with parameters frozen at aK. Skipping details we can conclude:

Theorem 1. *Under the stated conditions, $T_a = O(\log K)$, whenever finite.*

3. The Quasi-Stationary Phase

Once up in the vicinity of the carrying capacity, deterministic theory tells that population size is attracted to K and will stick there forever. Biological experience would lead us to expect a long period of lingering around K, and finally large deviation theory would indicate that the length of this era is of an exponential order in K. This was proved in [4] under the assumption of criticality in the strict sense, moment restrictions, and a Lipschitz condition on the criticality function,

$$\chi_z = b_z + h_z(m_z - 1) = L_z 1,$$

in terms of the operator L from Equation (1). Then criticality means that $\chi_z(a) = 0$ for all a, as soon as $z = K$. Somewhat carelessly we switch between dependence on population size and on the scaled population size ("density") $x = z/K$, writing χ_x, so that $\chi_1 = 0$. In this density notation, assume a Lipschitz condition in the neighbourhood of 1,so that there is a constant C such that

$$(3) \qquad\qquad |\chi_x| = |\chi_x - \chi_1| \le C|x - 1|.$$

Further we make a sort of exponential moment assumption, for discussion cf. [4]. (The reader more interested in principles than in technical detail, may jump directly to the theorem.) Let $\phi_z(t)(a) = \mathbb{E}_z[e^{tY(a)}]$ denote the moment generating function of the number $Y(a)$ of offspring at death of an a-aged individual splitting in a population of size z. For any K there should exist a population size $V_K > K$ such that

$$(4) \qquad (e^{1/K} - 1)b_z + (\phi_z(1/K)e^{-1/K} - 1)h_z \;\le\; 0, \quad \text{whenever } z > V_K,$$

and V_K/K is bounded for large K. When suitable, we use a superscript K to make the dependence of processes on K explicit.

Theorem 2. [4] *Assume that $X_0^K \to 1$ in probability. For any $\varepsilon > 0$, let $\tau^K = \inf\{t : |X_t^K - 1| > \varepsilon\}$. Suppose that the previous assumptions (3) and (4) hold and also that the number of offspring through splitting at death is bounded by some constant. Then $\mathbb{E}[\tau^K]$ is exponentially large in K, i.e. for some positive constants C, c*

$$\mathbb{E}[\tau^K] > Ce^{cK}.$$

Now, the question arises whether anything van be said about the constant c and a possible rate of convergence as $K \to \infty$ of $e^{-cK}T$, in a suitable sense. In the mentioned "barebones" case [4] of discrete time binary splitting, this is the case, thanks to a result by V. A. Vatutin (to appear, cf. also [5], though there is a misprint there):

Proposition 3. *For any $\epsilon > 0$ and any starting size $z \geq aK$, $0 < a < 1$,*

$$\mathbb{P}(e^{(c-\epsilon)K} < T < e^{(c+\epsilon)K}) \to 1,$$

as $K \to \infty$. In this,

$$c = \frac{a(1-a)^2}{8(1+a)}.$$

Simulations indicate that convergence in K is quick [5].

A value of a around $1/2$ then leads to $c \approx 0.01$ and for $K = 1000$ we obtain a seemingly large $e^{cK} \approx 20.000$. But this is generations, so shortlived cells or bacteria (cycle time around 20 minutes) in a small host will perish after a year or so. More longlived organisms, like humans, can persist for a very long time, provided we live cautiously.

4.   The Time of Descent

But ultimately any band around the carrying capacity will be left, and the population embark on its inevitable path to extinction. For classical, general subcritical branching processes starting from $aK, a > 0$, the time to extinction is $O(\log K)$ [3]. By a comparison argument the corresponding is true here.

Theorem 4. (Exact formulation and proof to appear) *For $0 < a < b < 1$,*

$$\mathbb{E}[T | no \ return \ to \ bK] = O(\log K).$$

REFERENCES

[1] P. Jagers. Branching Processes in Biology. Chichester, John Wiley & Sons, 1975.

[2] P. Jagers, F. C. Klebaner. Population-size-dependent and age-dependent branching processes. *Stoch. Proc. Appl.*, **87** (2000), 235–254.

[3] P. Jagers, F. C. Klebaner, S. Sagitov. On the Path to Exinction. *Proc. Nat. Acad. Sci.* (2007).

[4] P. Jagers, F. C. Klebaner. Population-size-dependent, age-structured branching processes linger around their carrying capacity. *J. Appl. Prob.* **48A** (2011), 249–260.

[5] F. C. Klebaner, S. Sagitov, V. A. Vatutin, P. Haccou, P. Jagers. Stochasticity in the adaptive dynamics of evolution: the bare bones. *J. Biol. Dyn.*, **5** (2011), 147–162.

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