

## 5.8 Population Size Dependent Processes

F.C. Klebaner

Recall that branching processes dependent on the population size are defined as Galton–Watson processes, but allowing that the offspring distribution may depend on the size of the mother’s generation,

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_{i,n}(Z_n). \quad (5.113)$$

Again, we use the somewhat inadvertent notation style commented upon in Section 5.6: here, the parentheses remind us of the dependence in distribution of reproduction on  $Z_n$ . In the same vein, denote by  $\xi(z)$  a random variable with the reproduction distribution

$$\mathbb{P}(\xi(z) = k) = p_k(z), \quad k = 0, 1, 2, \dots, \quad (5.114)$$

which is in force when the population size is  $z$ .

We address the extinction or explosion dichotomy first. If, for some population size  $z$ ,  $p_1(z) = 1$ , then once the population reaches this size, each member has one single offspring and the population size remains  $z$  forever. Barring this (quite artificial) possibility, extinction or explosion occurs, as in Theorem 5.7.

**Theorem 5.7** *Assume that for all  $z$ ,  $p_1(z) < 1$ . Then*

$$\mathbb{P}(Z_n \rightarrow \infty \text{ or } Z_n \rightarrow 0) = 1. \quad (5.115)$$

Provided  $\mathbb{P}(\xi(z) = 0) = p_0(z) > 0$  for all  $z$ , this is a consequence of the Metatheorem 5.1 [in its stricter formulation, take  $\delta(x) = \min_{1 \leq z \leq x} p_0(z)^z$ ]. Actually, the situation is simpler here because the process is a Markov chain. By general theory, it is enough to establish that any state  $z \neq 0$  is transient, meaning that having started with a population of size  $z$ , the probability of returning to the same size in the future is less than 1. This is clear, since there is always a positive probability of dying out; indeed, it is at least  $p_0(z)^z$  at level  $z$  and the population cannot recover from 0. The result remains true without the simplifying (but natural) assumption that  $p_0(z) > 0$  for all  $z$ , but the proof needs some extra concepts [see Fujimagari (1976); Klebaner (1984)].

It is important to have some information on the extinction probability. This is not simple, but in some cases there are straightforward results. For example, if

$$m(z) = \sum_k k p_k(z) \leq 1 \quad (5.116)$$

for all  $z$ , so that the population is subcritical or critical throughout, it dies out (barring the degenerate case mentioned). However, if it is supercritical with bounded variances, the extinction probability is less than 1.

The first statement is easy to see from the result on the extinction or explosion. First,

$$\mathbb{E}[Z_n] = \mathbb{E}[\mathbb{E}[Z_n|Z_{n-1}]] = \mathbb{E}[m(Z_{n-1})Z_{n-1}] \leq \mathbb{E}[Z_{n-1}]. \quad (5.117)$$

Second, we know that  $Z_n$  tends to some limit  $Z_\infty$ , which is either 0 or  $\infty$ . So we can use a result on mathematical expectations of positive variables, which states that the expectation of the limit does not exceed the limit of expectations (Fatou's lemma, see the Appendix) to conclude that in the case of (sub)critical reproduction  $\mathbb{E}[Z_\infty] \leq \mathbb{E}[Z_0]$ . Since the latter is finite, we must have that  $\mathbb{P}(Z_\infty = \infty) = 0$  and thus  $\mathbb{P}(Z_\infty = 0) = 1$ . In other words, extinction is certain.

Before we give general results on extinction, here is a simple result on generating functions that sometimes yields a useful bound on the extinction risk.

**Theorem 5.8** *Let  $f_z(s)$  be the generating function of offspring distribution when the population size is  $z$ . Assume that for all  $z$  and some  $u > 0$*

$$\int_0^1 (f_z(s))^z s^{u-1} ds \leq \frac{1}{z+u}. \quad (5.118)$$

*Then, the extinction probability does not exceed  $u/(z_0 + u)$ , where  $z_0$  is the non-random starting population.*

The proof is that for a non-negative random variable  $X$  with generating function  $f(s)$

$$\mathbb{E}\left[\frac{1}{X+u}\right] = \mathbb{E}\left[\int_0^1 s^{X+u-1} ds\right] = \int_0^1 f(s)s^{u-1} ds, \quad (5.119)$$

obtained by interchanging the order of expectation and integral.

Together with the condition of the theorem, this yields

$$\mathbb{E}\left[\frac{1}{Z_n+u} \mid Z_{n-1} = z\right] = \int_0^1 (f_z(s))^z s^{u-1} ds \leq \frac{1}{z+u}. \quad (5.120)$$

Taking expectations of this results in

$$\mathbb{E}\left[\frac{1}{Z_n+u}\right] \leq \mathbb{E}\left[\frac{1}{Z_{n-1}+u}\right], \quad (5.121)$$

which can be repeated to give

$$\mathbb{E}\left[\frac{1}{Z_n+u}\right] \leq \mathbb{E}\left[\frac{1}{Z_0+u}\right] = \frac{1}{z_0+u}. \quad (5.122)$$

As  $n \rightarrow \infty$ , either  $Z_n \rightarrow \infty$ , so that  $1/(Z_n + u) \rightarrow 1/(Z_\infty + u) = 0$  or else  $Z_n \rightarrow 0$  and  $1/(Z_n + u) \rightarrow 1/u$ . Thus, by Fatou's lemma (see the Appendix),

$$\frac{1}{z_0+u} \geq \liminf_{n \rightarrow \infty} \mathbb{E}\left[\frac{1}{Z_n+u}\right] \geq \mathbb{E}\left[\liminf_{n \rightarrow \infty} \frac{1}{Z_n+u}\right] = \mathbb{P}(Z_n \rightarrow 0)/u. \quad (5.123)$$

**Example 5.5: Near-critical binary splitting.** The theorem applies to binary splitting where the probability of division is  $p(z) = 1/2 + 1/(2z)$ , and  $q(z) = 1 - p(z)$  is the probability of no children, if population size is  $z$ . Thus,  $m(z) = 1 + 1/z$  and the process is supercritical, but approaches criticality as  $z$  increases.

The probability generating function of the offspring number is  $f_z(s) = q(z) + p(z)s^2$ . We take  $u = 2$  in Equation (5.118) to obtain

$$\begin{aligned} \mathbb{E}\left[\frac{1}{Z_{n+1} + 2} \mid Z_n = z\right] &= \int_0^1 (q(z) + p(z)s^2)^z s \, ds \\ &= 1/2 \int_0^1 (q(z) + p(z)y)^z \, dy \quad (s^2 = y) \\ &= 1/(2p(z)) \int_{q(z)}^1 t^z \, dt \quad (t = q(z) + p(z)y) \\ &\leq 1/(2p(z)) \int_0^1 t^z \, dt = 1/(2p(z)(z + 1)) \\ &= 1/(z + 2 + 1/z) < 1/(z + 2), \end{aligned} \tag{5.124}$$

which proves that Condition (5.118) is valid with  $u = 2$ . This means that the survival probability is at least 1/3 if  $Z_0 = 1$ , and close to 1 if the initial population is large, in sharp contrast to the strictly critical case. Indeed,  $Z_0 = 1000$  yields an extinction probability less than 2 promille.

◇ ◇ ◇

The following result is a classification theorem of Höpfner (1985). Recall that  $m(z)$  is the mean of offspring distribution when population size is  $z$  and write  $v(z) = \mathbb{E}[\xi(z)(\xi(z) - 1)]$ . The letters  $c, C, M, N$  denote positive constants.

**Theorem 5.9** *First assume that  $m(z) \leq 1 + c/z$  and  $\sigma^2 - M/z \leq v(z) < \infty$ , for all  $z > N$ . Then  $\mathbb{E}[\xi^2(z)] \leq C$  and  $\sigma^2 > 2c$  imply  $Q = 1$ , and  $\mathbb{E}[\xi^3(z)] \leq C$  and  $\sigma^2 = 2c$  also imply  $Q = 1$ .*

*Now assume that  $1 + c/z \leq m(z) < \infty$  and  $\sigma^2 + M/z \geq v(z)$ , for all  $z > N$ , and that  $\sigma^2 < 2c$ . Then  $Q < 1$ .*

In the framework of a more general growth model, Kersting (1986) gives the best possible results in this vein. Since the concepts used are too advanced for this book, the interested reader is referred to the article. These were applied by Klebaner (1990) to obtain conditions for extinction or survival in multi-type population size dependent Galton–Watson processes.

## 5.9 Effects of Sexual Reproduction

G. Alsmeyer

To examine the effect of sexual reproduction on extinction probabilities, we turn to the Galton–Watson process with mating, which is introduced in Section 2.8. Recall that in this model the  $n$ th generation consists of  $F_n$  females and  $M_n$  males, who form  $Z_n = \zeta(F_n, M_n)$  couples where  $F_n$  and  $M_n$  are random variables and  $\zeta$  is a

## References

*References in the book in which this section is published are integrated in a single list, which appears on pp. 295–305. For the purpose of this reprint, references cited in the section have been assembled below.*

Fujimagari T (1976). Controlled Galton–Watson process and its asymptotic behavior. *Kodai Mathematical Seminar Reports* **27**:11–18

Höpfner R (1985). On some classes of population size dependent Galton–Watson processes. *Journal of Applied Probability* **22**:25–36

Kersting G (1986). On recurrence and transience of growth models. *Journal of Applied Probability* **23**:614–625

Klebaner FC (1984). On population-size-dependent branching processes. *Advances in Applied Probability* **16**:30–55

Klebaner FC (1990). Conditions for the unlimited growth in multitype population size dependent Galton–Watson processes. *Bulletin of Mathematical Biology* **52**:527–534