

(Jagers 1997b)

$$\sum_{z=1}^{\infty} |m(z) - m| < \infty . \quad (6.90)$$

Thus, we can summarize that exponential growth tends to remain even in cases of dependence, provided the population is supercritical in the sense that the reproduction rate exceeds 1. That this holds true both for local dependences and for dependence upon the whole population indicates that it should be a robust phenomenon, valid in dependent structures of quite different kinds.

Let us underline that we view dependence, be it upon close relatives or upon the population globally, merely phenomenologically, as summarizing the underlying and possibly much more complex causal relations between external environment and internal physiology (cf. Kooijman 1993).

From the discussion in Section 5.2, we know that dependence upon population size cannot produce stationary populations. Now, it seems it cannot even produce growth slower than exponential. This is, however, not true, as we show in the following slightly more technical section. If the reproduction probability distribution approaches criticality as the population grows, and does so at the very same rate as the growth of the population (this basically means that the size of the deviation from criticality of the expected number of children in a population of size z is of the order $1/z$, as $z \rightarrow \infty$), then the population actually either dies out or else grows, not exponentially, but at a slower, linear rate – there are also other, polynomial growth rates.

6.5.3 Slowly growing populations

F.C. Klebaner

In this section we look at branching models in which the offspring distribution depends on the population size rather than the population density. In particular, we concentrate on the case in which mean offspring numbers stabilize as the population size grows larger and larger and approaches one, namely near-critical processes. The near-supercritical case is treated in Section 6.5.2.

Again,

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_{i,n}(Z_n) , \quad (6.91)$$

with the distribution of $\xi_{i,n}$ dependent on Z_n . If $m(z) = \mathbb{E}[\xi(z)]$ approaches m as $z \rightarrow \infty$, the process is called near-critical if $m = 1$ and near-supercritical if $m > 1$. Recall that a classic branching population survives with positive probability if and only if it is supercritical, and when it survives it grows at the rate m^n . Interesting phenomena occur in near-critical populations. Under some conditions, not only can they survive, as shown in Chapter 5, but also they can grow linearly, at the rate n , or more generally polynomially, at the rate n^α (see Klebaner 1983).

Linear growth occurs in the following situation: $m(z)$ should approach 1 as the population size z increases to infinity, and moreover it should approach 1 at the rate $1/z$. The variances $\sigma^2(z) = \text{Var}[\xi(z)]$ should approach some limit σ^2 . The condition on third moments of offspring distribution in Theorem 6.7 follows from the moments being bounded, as is certainly biologically reasonable.

Theorem 6.7 *Suppose that $z(m(z) - 1) \rightarrow c$, $\sigma^2(z) \rightarrow \sigma^2$, $\sigma^2 < 2c$, and that $\mathbb{E}[|\xi(z) - m(z)|^3]/\sqrt{z} \rightarrow 0$, all when $z \rightarrow \infty$. Then Z_n/n converges in distribution to some random variable, which is 0 with the extinction probability Q . Furthermore, conditioned on non-extinction, it equals c if $\sigma^2 = 0$, and if $\sigma^2 > 0$ it has a Gamma distribution with parameters $2c/\sigma^2$ and $2/\sigma^2$.*

Note that if the condition on the limit variance is violated and $\sigma^2 \geq 2c$, extinction occurs. Therefore, it can be said that such processes “live on the boundary between extinction and survival.” For definition of Gamma distributions, see the Appendix.

Under somewhat different conditions, this result was given by Klebaner (1984), Höpfner (1985), and Kersting (1992), who obtained the best possible form.

Example 6.5 Recall the example of binary splitting from Section 5.8, in which the probability of division into two is $p(z) = 1/2 + 1/(2z)$, given that the population size is z . In this case, as shown, there is a positive chance of survival. Further, $m(z) = 2p(z) = 1 + 1/z$, and $z(m(z) - 1) \rightarrow 1$, $\sigma^2(z) = 4p(z) - m^2(z) \rightarrow 1$. The third moments clearly are bounded by $2^3 = 8$. Hence, if the population does not die out, Z_n/n converges to a $\Gamma(2, 2)$ variable (again, see the Appendix).



Example 6.6 A further application is provided by polymerase chain reaction (PCR) models, which have the mean “offspring” number per molecule

$$m(z) = 1 \times (1 - p(z)) + 2 \times p(z) = 1 + p(z) = 1 + \frac{K}{K + z}, \quad (6.92)$$

when population size is z , provided Michaelis–Menten kinetics can be assumed (see Section 7.5). The variance of the offspring distribution of any single individual is

$$\sigma^2(z) = 4p(z) + 1 - p(z) - m^2(z) = p(z)(1 - p(z)) = \frac{Kz}{(K + z)^2}. \quad (6.93)$$

Since the offspring number per molecule does not exceed two, the third moment is, clearly, bounded, and thus satisfies the condition of Theorem 6.7. It follows from Theorem 6.7 that

$$Z_n/n \rightarrow K \quad (6.94)$$

in probability as $n \rightarrow \infty$. As we show later, convergence actually holds in stronger senses.



A more general, polynomial growth may occur in near-critical processes. For different types of growth, including polynomial, see Klebaner (1989a) and Kersting (1992).

Theorem 6.8 *Suppose that there exist constants $0 < c < \sigma^2/2$ and $\alpha < 1$, such that as $z \rightarrow \infty$,*

$$z^{1-\alpha}(m(z) - 1) \rightarrow c, \sigma^2(z)/z^\alpha \rightarrow \sigma^2 > 0, \tag{6.95}$$

$$\mathbb{E}[|\xi(z) - m(z)|^3]/z^{1/2+\alpha} \rightarrow 0. \tag{6.96}$$

Then $Z_n/n^{1/(1-\alpha)}$ converges in distribution. The limit W equals zero only if the population dies out. If this does not occur, the limit has a generalized Gamma distribution, that is, $W^{(1-\alpha)}$ is Gamma with parameters $(2c - \sigma^2\alpha)/(\sigma^2 - \sigma^2\alpha)$ and $2/(\sigma^2(1 - \alpha)^2)$.

Polynomial growth typically occurs in a situation in which the number of offspring is 0 with a very large probability and very large with a very small probability, as illustrated in the Example 6.7.

Example 6.7 Given that the population size is z , let the number of offspring be $a(z) = [\sigma^2 z^\alpha]$, where the brackets denote the integer part of a number and $\alpha < 1/2$, with probability $p(z) = 1/a(z) + c/(a(z)z^{1-\alpha})$ and zero with the complementary probability. Then $m(z) = a(z)p(z)$ satisfies the assumption, as do the variances and third moment. Therefore, conditioned on non-extinction, $Z_n/n^{1/(1-\alpha)}$ converges to a limit that has a generalized Gamma distribution. This example might be appropriate for modelling insects, in cases where there is a great risk of larvae dying, but otherwise they give birth to a large number of individuals.



For near-supercritical processes, $m(z) \rightarrow m > 1$, Theorem 5.9 (Section 5.8) gives sharp conditions for geometric growth with rate m^n . A description of growth rates close to exponential in near-supercritical processes is given in Küster (1985) and Keller *et al.* (1987).

These processes are studied in the framework of a more general growth model,

$$X_{n+1} = X_n + g(X_n)(1 + \xi_{n+1}), \tag{6.97}$$

where $X_0 > 0$, $g(t)$ is strictly positive, $g(t)/t \rightarrow 0$ as $t \rightarrow \infty$, and (ξ_n) is a so-called zero-mean, square-integrable martingale difference sequence, that is

$$\mathbb{E}[\xi_{n+1} | X_0, \dots, X_n] = 0 \tag{6.98}$$

and

$$\mathbb{E}[\xi_{n+1}^2 | X_0, \dots, X_n] = \sigma^2(X_n). \tag{6.99}$$

Under several regularity conditions, the authors show that extinction or explosion occurs, that is, $\lim_{n \rightarrow \infty} X_n = 0$ or $\lim_{n \rightarrow \infty} X_n = \infty$ and that $\mathbb{P}(\lim_{n \rightarrow \infty} X_n \rightarrow \infty) > 0$. The growth rate of the (X_n) is characterized with help of the function $G(t) = \int_1^t ds/g(s)$ (which tends to ∞ as $t \rightarrow \infty$). If $A = \{X_n \rightarrow \infty\}$, then $G(X_n)/n \rightarrow 1$ with probability 1 on A . It is also possible to compare the stochastic recursion Equation (6.97) to the deterministic one. Let $a_0 = 1$ and $a_{n+1} = a_n + g(a_n)$ define the deterministic solution of Equation (6.97), then it is possible to estimate how closely X_n tracks a_n [see Keller *et al.* (1987) for details].

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.

- Höpfner R (1985). On some classes of population size dependent Galton–Watson processes. *Journal of Applied Probability* **22**:25–36
- Keller G, Kersting G & Rösler U (1987). On the asymptotic behaviour of discrete time stochastic growth processes. *Annals of Probability* **15**:305–343
- Kersting G (1992). Asymptotic Γ distribution for stochastic difference equations. *Stochastic Processes and their Applications* **40**:15–28
- Klebaner FC (1983). Population-size-dependent branching process with linear rate of growth. *Journal of Applied Probability* **20**:242–250
- Klebaner FC (1984). On population-size-dependent branching processes. *Advances in Applied Probability* **16**:30–55
- Klebaner FC (1989a). Stochastic difference equations and generalized gamma distributions. *Annals of Probability* **17**:178–188
- Küster P (1985). Asymptotic growth of controlled Galton–Watson processes. *Annals of Probability* **13**:1157–1178