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

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

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

Now assume that $1 + c/z \le m(z) < \infty$ *and* $\sigma^2 + M/z \ge v(z)$, *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 nth 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 ζ is a

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Alsmeyer G (2005). Effects of Sexual Reproduction. In: Branching Processes: Variation, Growth, and Extinction of Populations, Haccou P, Jagers P & Vatutin VA, pp. 135–145. Cambridge University Press.

deterministic function, called a *mating function*. Each couple produces offspring independently of all other couples and according to the same distribution. Thus, let for each couple $p_{j,k}$ denote the probability of producing j female and k male children. With X_k and Y_k denoting, respectively, the number of female and male offspring of the kth couple of the nth generation (labeled in arbitrary fashion), we arrive at

$$F_{n+1} = \sum_{k=1}^{Z_n} X_k \quad \text{and} \quad M_{n+1} = \sum_{k=1}^{Z_n} Y_k \tag{5.125}$$

for $n \geq 0$, where the (X_k, Y_k) are independent and identically distributed. This is the familiar structure for the Galton–Watson branching process with the one, but important, difference that here the summation ranges over the number of couples of the preceding generation. Choosing the "asexual" mating function $\zeta(x, y) = x$, we see that Z_n just equals the number of females in the nth generation ($Z_n = F_n$ for all $n \geq 0$) and is, indeed, a classic branching process.

From a mathematical viewpoint it is desirable to restrict the class of offspring distributions to facilitate explicit computations. Daley (1968) gave two alternative possibilities:

Assumption 5.2 *Conditionally on the total number of offspring, their sex is determined at random (analogously to flipping a, possibly biased, coin). More formally, if $\hat{p}_{j+k}$ denotes the probability that a couple produces $j + k$ children, and if the probability that a child is female equals θ, then*

$$p_{j,k} = \binom{j+k}{j} \theta^j (1-\theta)^k \, \hat{p}_{j+k} \tag{5.126}$$

for all $j, k \geq 0$.

Assumption 5.3 *Another possibility is that the numbers of male and female offspring are independent with a possibly different distribution. In this case*

$$p_{j,k} = p_j^F \, p_k^M \tag{5.127}$$

for all $j, k \geq 0$, where p_j^F and p_k^M denote the probabilities that a couple has, respectively, j female and k male children.

The mechanism that corresponds to Assumption 5.2 is most common in mammals, and occurs in humans with $\theta = 0.5$. Assumption 5.3 may be reasonable in situations with environmental sex determination, such as temperature dependence in many reptiles [for examples, see Bull (1983)]. The two mechanisms are equivalent for Poisson-distributed numbers of male and female offspring, so Assumption 5.3 with $(p_j^F)_{j\geq 0}$ and $(p_j^M)_{j\geq 0}$ Poisson distributions with means m^F and m^M, respectively, is equivalent to Assumption 5.2 with the Poisson distribution $(\hat{p}_j)_{j\geq 0}$ with mean $m^F + m^M$, and $\theta = m^F/(m^F + m^M)$.

Let us stipulate without further discussion that hereafter $(p_{j,k})_{j,k\geq 0}$ always satisfies Assumption 5.2 or 5.3 and, further, that there is a positive probability of producing offspring that are of one sex only, that is,

$$\max(p_{0,\bullet}, p_{\bullet,0}) > 0 \,, \tag{5.128}$$

where $p_{0,\bullet} = \sum_{k\geq 0} p_{0,k}$ and $p_{\bullet,0} = \sum_{j\geq 0} p_{j,0}$ denote the respective probabilities that a couple has only male or only female offspring. This condition holds automatically under Assumption 5.2 because $0 < \theta < 1$, and is equivalent to $\max(p_0^F, p_0^M) > 0$ under Assumption 5.3. As before, we assume that the mating function ζ is common sense and superadditive (see Section 2.8).

5.9.1 Criticality

We now turn to the fundamental question of finding conditions that guarantee certain ultimate extinction of a Galton–Watson process with mating $(Z_n)_{n\geq 0}$. To be more precise, let

$$Q_j \ = \mathbb{P}(Z_n = 0 \text{ eventually} | Z_0 = j) \tag{5.129}$$

denote the extinction probability given $j \geq 1$ ancestor couples. Then the question in its most ambitious form may be restated as: Is there an intuitive condition for $Q_1 = Q_2 = \cdots = 1$, as for the simple Galton–Watson process, where we know that certain extinction occurs if, and only if, each individual produces at most one child on average and has a positive chance of having no children?

The following example, from Hull (1982), shows that one cannot expect an equally simple answer for processes with sexual reproduction. Consider the mating function $\zeta(x, y) = 0$ if $x = 0$ or $y = 0$, and $\zeta(x, y) = x+y-1$ otherwise. Let $p_{j,k}$ be of the form of Equation (5.126) for some $0 < \theta < 1$ and with $(\hat{p}_j)_{j\geq 0}$ defined through $\hat{p}_3 = 1$, and hence $\hat{p}_j = 0$ otherwise. Then, every couple has exactly three children. Nonetheless, extinction occurs if, for some $n \geq 0$, all couples of the nth generation produce only female or only male offspring. By comparison with a process of an inbreeding population in which couples are formed only by children of the same parents, Hull showed that $Q_j < 1$ for all $j \geq 1$ and any choice of θ (see Theorem 5.10 and its proof in Box 5.3). This may come as a surprise because

$$m \ = \ \mathbb{E}[Z_1 | Z_0 = 1] \ = \ 2(1 - \theta^3 - (1 - \theta)^3) \tag{5.130}$$

is strictly less than 1 if $\theta = 0.8$. However, as pointed out later by Bruss (1984), more relevant here are the *average unit reproduction means*

$$m_j \ = \frac{1}{j}\, \mathbb{E}[Z_{n+1} | Z_n = j] \,, \quad j \geq 1 \,, \tag{5.131}$$

which give the mean population growth rates per generation for the various levels j. For the simple Galton–Watson process this is disguised by the lucky coincidence that m_j does not depend on j. In the given example,

$$m_j \ = \ \frac{3j-1}{j}(1 - \theta^{3j} - (1-\theta)^{3j}) \,, \tag{5.132}$$

which, for any choice of θ, increases to 3 as j tends to infinity. In the case $\theta = 0.8$, we thus see that the population, when originating from one ancestor couple, can actually survive because, with positive probability, it eventually reaches a level at which the growth becomes supercritical ($m_j > 1$, for all sufficiently large j).

It is quite intuitive, and actually confirmed by the following result of Daley *et al.* (1986), that this latter observation holds true more generally.

Theorem 5.10 *For a Galton–Watson process* $(Z_n)_{n\geq 0}$ *with a common sense, superadditive mating function* ζ*, the average reproduction means* m_j *are convergent to the limit* $m_\infty = \sup_{k\geq 1} m_k$*. Furthermore,* $m_\infty \leq 1$ *implies certain extinction for any initial population size (i.e.,* $Q_1 = Q_2 = \cdots = 1$*), while in the case* $m_\infty > 1$ *(ultimate supercriticality) the population survives with positive probability for a sufficiently large initial population size, in fact* $1 > Q_{i_0} \geq Q_{i_0+1} \geq \cdots$ *for some positive integer* i_0*.*

For those readers who wonder whether there are examples of ultimately supercritical processes with common sense superadditive mating functions that die out if the initial population size is too small, we note that this happens, for instance, if the mating function ζ is chosen such that $\zeta(x, y) = 0$ whenever x or y is less than some (arbitrarily chosen) threshold. Other, less trivial examples can also be given, but further discussion is omitted because the biological relevance of any such example seems doubtful. We add in support of the latter statement that, whenever the considered population has a positive chance of increase at any given level i, formally stated as $\mathbb{P}(Z_{n+1} > i | Z_n = i) > 0$ for all $i \in \mathbb{N}$, then ultimate supercriticality implies a positive chance of survival for *all* initial population sizes, so $i_0 = 1$ and $1 > Q_1 \geq Q_2 \geq \cdots$. Since, by the Strong Law of Large Numbers (see the Appendix), $\bar{X}_j = j^{-1}\sum_{i=1}^{j} X_i$ and $\bar{Y}_j = j^{-1}\sum_{i=1}^{j} Y_i$ tend to the average numbers of female and male children per couple, m^F and m^M, writing

$$m_\infty = \lim_{j\to\infty} \mathbb{E}\big[\zeta\big(\sum_{i=1}^{j} X_i, \sum_{i=1}^{j} Y_i\big)\big]/j = \lim_{j\to\infty} \mathbb{E}\big[\zeta\big(j\bar{X}_j, j\bar{Y}_j\big)\big]/j\ , \tag{5.133}$$

it should not be surprising that one can show that

$$m_\infty = \lim_{j\to\infty} \mathbb{E}\big[\zeta\big(jm^F, jm^M\big)\big]/j = r(m^F, m^M) \tag{5.134}$$

for a suitable function r (see Daley *et al.* 1986, Lemma 2.3). We note in passing the technical point that m^F and m^M need not be integers, but that, by linear interpolation, $\zeta(x, y)$ can always be defined for all pairs (x, y) of non-negative numbers without losing superadditivity. For the examples given in Section 2.8 this is clear anyway. Although it often may be hard to determine r explicitly, there are many examples of ζ, including ours, for which this is easy. In fact, $\zeta(x, y) = \min(x, dy)$ implies $r = \zeta$ and $m_\infty = \min(m^F, dm^M)$ and $\zeta(x, y) = x\min(1, y)$ implies $r(x, y) = x$ and $m_\infty = m^F$.

Box 5.3 Proof of Theorem 5.10

In the following we present the main arguments of the proof, without technicalities. The first observation to make is that

$$\mathbb{P}(Z_{n+1} = j | Z_n = i) = \mathbb{P}\Big(\zeta\big(\sum_{k=1}^{i} X_{n+1,k}, \sum_{k=1}^{i} Y_{n+1,k}\big) = j\Big) \tag{a}$$

and, since the mating function ζ is monotonic in each argument, this implies

$$\mathbb{P}(Z_1 > k | Z_0 = i) = \mathbb{P}\Big(\zeta\big(\sum_{j=1}^{i} X_j, \sum_{j=1}^{i} Y_j\big) > k\Big) \leq \mathbb{P}\Big(\zeta\big(\sum_{j=1}^{i+1} X_j, \sum_{j=1}^{i+1} Y_j\big) > k\Big)$$
$$= \mathbb{P}(Z_1 > k | Z_0 = i+1) \tag{b}$$

for all $i, k \in I\!N_0$. So the probability of exceeding a size k in the next generation forms an increasing function of the current population size. A Markov chain with this property is called *stochastically monotone*. By an easy inductive argument, one can prove that Equation (b) generalizes to

$$\mathbb{P}(Z_n > k | Z_0 = i) \leq \mathbb{P}(Z_n > k | Z_0 = i+1) \tag{c}$$

for all $i, k = 0, 1, 2, \ldots$ and $n = 1, 2, \ldots$, which in turn yields the important fact that the extinction probability Q_i is a decreasing function of the initial population size i. Namely, by letting n tend to infinity in Equation (c),

$$1 - Q_i = \lim_{n\to\infty} \mathbb{P}(Z_n > 0 | Z_0 = i) \leq \lim_{n\to\infty} \mathbb{P}(Z_n > 0 | Z_0 = i+1) = 1 - Q_{i+1} \tag{d}$$

for all $i \in I\!N_0$. For a more intuitive comparison argument, suppose the population starts with $i + 1$ ancestor couples ($Z_0 = i + 1$). Choose an arbitrary subset of i couples and denote by $(Z'_n)_{n\geq 0}$ the process based on this subset, hence $Z'_0 = i$. Then the Z_1 couples that form the first generation of the original population are those formed by the offspring of the i ancestor couples of the subpopulation plus, generally, some more because of the one additional ancestor couple in the original population and the monotonicity of the mating function. This shows $Z'_1 \leq Z_1$ and finally leads to the conclusion that $Z'_n \leq Z_n$ for all $n \geq 0$ when repeating the argument for the subsequent generations. Since the extinction probabilities of $(Z_n)_{n\geq 0}$ and $(Z'_n)_{n\geq 0}$ are Q_{i+1} and Q_i, respectively, the inequality $Q_i \geq Q_{i+1}$ follows as a consequence.

We now show that m_j converges to $m_\infty = \sup_{k\geq 1} m_k$. Indeed, from the definition in Equation (5.131)

$$(j + k)m_{j+k} = \mathbb{E}[Z_1 | Z_0 = j + k] = \mathbb{E}\Big[\zeta\big(\sum_{l=1}^{j+k} X_l, \sum_{l=1}^{j+k} Y_l\big)\Big] \tag{e}$$

and from the superadditivity of ζ, the result is larger than or equal to

$$\mathbb{E}\Big[\zeta\big(\sum_{l=1}^{j} X_l, \sum_{l=1}^{j} Y_l\big)\Big] + \mathbb{E}\Big[\zeta\big(\sum_{l=j+1}^{j+k} X_l, \sum_{l=j+1}^{j+k} Y_l\big)\Big]. \tag{f}$$

continued

Box 5.3 *continued*

From the independence and identical distribution of the offspring variables (X_l, Y_l), it follows that this equals

$$\mathbb{E}\Big[\zeta\big(\sum_{l=1}^{j} X_l, \sum_{l=1}^{j} Y_l\big)\Big] + \mathbb{E}\Big[\zeta\big(\sum_{l=1}^{k} X_l, \sum_{l=1}^{k} Y_l\big)\Big]$$
$$= \mathbb{E}[Z_1|Z_0 = j] + \mathbb{E}[Z_1|Z_0 = k] = jm_j + km_k \tag{g}$$

for all $j, k \geq 1$. Combining Equation (e) with Equation (g), we find that $(j + k) m_{j+k} \geq jm_j + km_k$ for all $j, k \geq 1$, which implies that jm_j is superadditive. Applying standard results on superadditive functions to $(jm_j)_{j\geq 1}$ (e.g., Hille and Phillips 1957) then yields the asserted convergence of the m_j to $m_\infty = \sup_{k\geq 1} m_k$.

Suppose now that $m_\infty \leq 1$ and thus $m_j \leq 1$ for all $j \geq 1$. Then

$$\mathbb{E}[Z_{n+1}|Z_n = i] = im_i \leq i \tag{h}$$

holds for all $i, n \geq 0$. A stochastic sequence with this property is called a supermartingale (see the Appendix). A fundamental result from the theory of stochastic processes says that every non-negative supermartingale converges to a finite random variable, hence $Z_n \to Z_\infty$ (for any given initial population size). However, Z_∞ must then be identical to 0 by the extinction–explosion dichotomy (see Section 5.2), and so $Q_1 = Q_2 = \cdots = 1$, as asserted.

To see that $Q_i < 1$ for all sufficiently large i in the case $m_\infty > 1$ is more difficult and too technical to be presented here. However, a rather simple argument from Hull (1982) exists under the stronger condition $m_1 > 1$, and is again based on a comparison of $(Z_n)_{n\geq 0}$ with another process, a supercritical Galton–Watson process. Define $Z'_0 = Z_0$ and then, recursively,

$$Z'_n = \sum_{j=1}^{Z'_{n-1}} \zeta(X_j, Y_j) \tag{i}$$

for $n \geq 2$. One may think of $(Z'_n)_{n\geq 0}$ as describing an inbreeding population in which couples are formed according to the same mating function, but only by children of the same parents. The superadditivity of ζ implies

$$Z'_1 = \sum_{j=1}^{Z_0} \zeta(X_j, Y_j) \leq \zeta\big(\sum_{j=1}^{Z_0} X_j, \sum_{j=1}^{Z_0} Y_j\big) = Z_1 , \tag{j}$$

and then, inductively, $Z'_n \leq Z_n$ for all $n \geq 0$. Since all $\zeta(X_j, Y_j)$ are independent with the same distribution $(p_k)_{k\geq 0}$, say, $(Z'_n)_{n\geq 0}$ is distributed as a simple Galton–Watson process with offspring distribution $(p_k)_{k\geq 0}$. It is further supercritical because $\mathbb{E}[\zeta(X_1, Y_1)] = \mathbb{E}[Z_1|Z_0 = 1] = m_1 > 1$. Consequently, $(Z'_n)_{n\geq 0}$ survives with positive probability for any initial population size and so $(Z_n)_{n\geq 0}$ also does (i.e., $1 > Q_1 \geq Q_2 \geq \cdots$).

5.9.2 Sexual versus asexual reproduction: The extinction probability ratio

Given a large initial population size, how does mating affect the extinction probability as compared to the asexual case? This interesting and natural question appears to be a hard one from a mathematical point of view, which may be why only very few contributions to this subject are found in the literature, namely Daley *et al.* (1986) and Alsmeyer and Rösler (1996, 2002). For the classic basic branching process, the extinction probability Q_i given an initial size i satisfies $Q_i = Q_1^i$ and can be calculated exactly because Q_1 is found as the smallest solution in [0, 1] to the equation $f(s) = s$, where $f(s) = \sum_{j \geq 0} p_j s^j$ denotes the generating function of the offspring distribution. Unfortunately, there is no such simple way to compute Q_i for Galton–Watson processes with mating, whatever the choice of the mating function.

Daley *et al.* (1986) suggest a finite Markov chain approximation, which is described roughly as follows. Let $(Z_n)_{n \geq 0}$ be a Galton–Watson process with superadditive mating function ζ and note that $(Z_n)_{n \geq 0}$ forms a temporally homogeneous Markov chain with transition matrix $P = (P_{ij})_{i,j \geq 0}$, that is,

$$P_{ij} \; = \; \mathbb{P}(Z_n = j | Z_{n-1} = i) \tag{5.135}$$

denotes the conditional probability that, at any time $n = 0, 1, 2, \ldots$, the population size changes from i to j. The state 0 is absorbing and thus $P_{00} = 1$. The extinction–explosion dichotomy further implies that, in the case of survival, the chain is asymptotically absorbed at ∞. Moreover, the latter is more and more likely to happen if the initial population size becomes large. Hence, the probability of extinction (absorption at 0) should only change very little if, for some integer N considerably larger than the initial state, $(Z_n)_{n \geq 0}$ is replaced with the finite Markov chain $(Z_n(N))_{n \geq 0}$, say, which evolves exactly as $(Z_n)_{n \geq 0}$ until a state $N + i$, $i \geq 1$, is hit, in which case the latter chain is absorbed at N. The extinction probabilities of both chains then only differ by the probability of the rare event that $(Z_n)_{n \geq 0}$ dies out after exceeding the high level N. However, extinction probabilities for the finite Markov chain $(Z_n(N))_{n \geq 0}$ can be obtained as the solutions to a *finite* system of linear equations.

To make this precise, fix a large integer N and let $(Z_n(N))_{n \geq 0}$ be defined as

$$Z_n(N) = Z_{\min(n, T(N))} = \begin{cases} Z_n, & \text{if } n < T(N) \\ Z_{T(N)}, & \text{if } n \geq T(N) \end{cases}, \tag{5.136}$$

where $T(N)$ is the first time k is such that $Z_k > N$. This chain has the transition matrix

$$P(N) = \begin{pmatrix} 1 & 0 & \ldots & 0 & 0 \\ P_{10} & P_{11} & \ldots & P_{1N} & 1 - \sum_{i=0}^{N} P_{1i} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ P_{N0} & P_{N1} & \ldots & P_{NN} & 1 - \sum_{i=0}^{N} P_{Ni} \\ 0 & 0 & \ldots & 0 & 1 \end{pmatrix}. \tag{5.137}$$

The extinction probabilities $Q_i(N) = \mathbb{P}(Z_n(N) = 0 \text{ eventually}|Z_0(N) = i)$, $i = 1, \dots, n$, satisfy the system of linear equations

$$Q_i(N) = P_{i0} + \sum_{j=1}^{N} P_{ij} Q_j(N), \quad i = 1, \dots, N, \tag{5.138}$$

which in matrix form reads

$$Q(N) = (I - R(N))^{-1} P_0(N), \tag{5.139}$$

where

$$Q(N) = \begin{pmatrix} Q_1(N) \\ \vdots \\ Q_N(N) \end{pmatrix}, \quad P_0(N) = \begin{pmatrix} P_{10} \\ \vdots \\ P_{N0} \end{pmatrix}, \quad R(N) = \begin{pmatrix} P_{11} & \dots & P_{1N} \\ \vdots & \ddots & \vdots \\ P_{N1} & \dots & P_{NN} \end{pmatrix}, \tag{5.140}$$

and I is the identity matrix. Note that

$$(I - R(N))^{-1} = I + R(N) + R(N)^2 + \cdots. \tag{5.141}$$

The following result from Daley *et al.* (1986) provides an estimate for $Q_i - Q_i(N)$ for $N \geq i$ and is stated without proof.

Theorem 5.11 *Given a Galton–Watson process $(Z_n)_{n\geq 0}$ with superadditive mating function,*

$$Q_i(i + j - 1) \leq Q_i \leq \min\left(1, \frac{Q_i(i + j - 1)}{1 - Q_j(i + j - 1)}\right) \tag{5.142}$$

for all $i, j \geq 1$.

Daley *et al.* (1986) used this finite chain approximation to compute the extinction probabilities Q_i of supercritical processes with monogamous or (unilateral) promiscuous mating functions for various initial generation sizes i. The numbers of female and male offspring per individual were assumed to be independent, with a Poisson distribution of mean 1.2, that is,

$$p_j^F = p_j^M = e^{-1.2} \frac{1.2^j}{j!} \quad j = 0, 1, 2, \dots. \tag{5.143}$$

The simple (asexual) branching process with this offspring distribution has extinction probabilities Q^i for $i \geq 1$, where $Q = 0.6863$. These values can be compared to the respective extinction probabilities Q_i for the monogamous or (unilateral) promiscuous branching processes, which are clearly larger. Based on the numbers in Daley *et al.* (1986), Table 5.6 shows the values of the extinction probability ratio $R_i = Q_i/0.6863^i$ for various initial generation sizes i.

In the monogamous case R_i apparently tends to infinity. Daley *et al.* (1986) note that there does not appear to be a simple way to find the precise asymptotic

Table 5.6 Extinction probability ratios for various initial generation sizes.

Initial generation size	Mating type Asexual	Monogamous	Promiscuous
i	0.6863^i	$R_i = Q_i/0.6863^i$	
1	0.6863	1.4530	1.2439
2	0.4710	2.0964	1.3161
3	0.3233	2.9938	1.3300
4	0.2219	4.2231	1.3308
5	0.1523	5.8779	1.3300
6	0.1045	8.0699	1.3292
10	0.2318×10^{-1}	25.0216	1.3296
20	0.5374×10^{-3}	204.1310	1.3295
40	0.2888×10^{-6}	2637.1191	1.3296
60	0.1552×10^{-9}	12847.9381	1.3293

behavior of R_i, but that, by a very rough heuristic argument based on the Central Limit Theorem, it seems plausible that $R_i \approx \exp(c\sqrt{i})$ for some $c > 0$ and sufficiently large i. They also point out that, in the promiscuous case, R_i seems to converge rapidly to about 1.33, but do not give a theoretical explanation for the particular value. However, convergence of R_i is quite plausible because the promiscuous process behaves exactly like the asexual process that pertains to the female subpopulation, as long as at least one male is born in each generation. An additional risk of extinction is caused only by the probability that a generation may have no male offspring at all, which becomes more and more unlikely for increasing initial population sizes. Based on these observations Alsmeyer and Rösler (1996, 2002) provide a deeper analysis of promiscuous processes with offspring distributions that satisfy Assumption 5.3. Although the mathematical details are far beyond the scope of this survey, as they involve potential theoretic aspects of branching processes, we summarize the major findings from these authors in Theorem 5.12.

So we consider a Galton–Watson process with (unilateral) promiscuous mating $(Z_n)_{n\geq0}$ that has probabilities $p_{j,k} = p_j^F p_k^M$ of having j daughters and k sons, respectively, per couple. Since Z_n equals the number of females in the nth generation, as long as at least one male is alive it follows easily with Assumption 5.3 that the extinction probabilities Q_i depend on the male offspring distribution $(p_k^M)_{k\geq0}$ only through p_0^M, the probability that a couple has no male offspring. Let $f(s) = \sum_{j\geq0} p_j^F s^j$ be the generating function of the female offspring distribution $(p_j^F)_{j\geq0}$, f_n its nth iterate (see Section 5.3), and Q the extinction probability of the associated simple Galton–Watson process, say $(F_n)_{n\geq0}$, with this offspring distribution. Hence, Q is the smallest solution of $f(Q) = Q$ in [0, 1], and $f_n(s) \uparrow Q$ for each $s \leq Q$.

Theorem 5.12 *Suppose that* $m^F = \sum_{j\geq1} jp_j^F > 1$ *and* $\kappa = p_0^M < 1$.

(a) The following assertions hold true for all $i \geq 1$*:*

1. *If* $\kappa < p_0^F$, *then*

$$1 \le R_i \le 1 + \frac{\kappa}{p_0^F} \,; \tag{5.144}$$

2. *If* $\kappa = p_0^F$, *then*

$$1 + \frac{1 - Q}{1 + Q - p_0^F} \le R_i \le 2 \,; \tag{5.145}$$

3. *If* $p_0^F < \kappa < Q$, *then*

$$1 + \frac{\kappa(1 - Q)}{\kappa Q + (1 - \kappa) p_0^F} \le R_i \le (n + 2)\left(\frac{1}{1 - \kappa} + \frac{p_0^F}{\kappa}\right), \tag{5.146}$$

where n is determined through $f_n(p_0^F) < \kappa \le f_{n+1}(p_0^F)$;

4. *If* $\kappa = Q$, *then*

$$\frac{1 - Q}{Q(a_1 - Q) + (1 - Q)} \le \frac{R_i}{a_i} \le \frac{1}{1 - q} + \frac{p_0}{q}, \tag{5.147}$$

where $a_i = \mathbb{E}(\tau | \tau < \infty, F_0 = i)$ *and* $\tau = \inf\{n \ge 0 : F_n = 0\}$;

5. *If* $\kappa > Q$, *then*

$$1 \le \frac{Q_i}{\kappa^i} \le 1 + \frac{f(\kappa)}{\kappa - f(\kappa)} \,. \tag{5.148}$$

(b) If $0 < \kappa < Q$, *then convergence of* R_i *does not hold in general, while*

$$\lim_{i\to\infty} \ln\left(\frac{1}{f'(Q)}\right)\frac{R_i}{a_i} = \lim_{i\to\infty} \frac{R_i}{\ln i} = 1 \quad \text{if } \kappa = Q \,, \tag{5.149}$$

and

$$\lim_{i\to\infty} \frac{R_i}{\kappa^i} = 1 \quad \text{if } \kappa > Q \,. \tag{5.150}$$

The most intriguing result stated in Theorem 5.12 is that for $0 < \kappa < Q$ convergence of R_i fails to hold in general. This is even more surprising considering that all computational studies of R_i for this case indicate the contrary, namely a rapid convergence to some finite value, as in the above example studied by Daley *et al.* (1986); see Alsmeyer and Rösler (1996) for some examples. The disclosed phenomenon belongs to the class of so-called *near-constancy phenomena*, which also show up in other problems in the theory of branching processes (see also Biggins and Nadarajah 1993). It means that a considered sequence is seemingly convergent, but actually oscillates in a very small range (of the order 10^{-4} or smaller). The convergence results, Equation (5.149) and Equation (5.150), are much more appealing to intuitive thinking, their interpretation being that for $\kappa \ge Q$, the extinction of a population with large initial size is more likely to be caused by the disappearance of males than that of females.

Box 5.4 Lotka's data reconsidered by Hull

Lotka (1931a, 1931b) calculated the extinction probability of a male line of descent from one newborn male. Using data from a US census of 1920, he arrived at the conclusion that this risk equals 0.8715. His calculation, however, was based on an asexual branching process model. Recently, Hull (2001) corrected the estimate, using a branching process with monogamous mating. He used the offspring distribution given by Lotka and sex determination according to Assumption 5.2. From the same census data, he estimated that the probability of producing a female child, θ, equaled 0.485. With the numerical approach developed by Daley *et al.* (1986) and outlined above, he arrived at an estimated extinction probability of 0.9958, obviously much larger than Lotka's estimate. This would be a grim prospect for the survival of family names (the application that Lotka had in mind). As Hull notes, however, this analysis is based on the assumption of a single mating unit in the initial population. Moreover, a particular name that originates from a single family has a higher survival chance when other mating units produce females to act as mates for future generations, especially when males from that family are highly esteemed (Hull 1998).

5.10 Environmental Variation Revisited

In this section we reconsider the effect of environmental variation. Some examples of branching process models in varying environments were introduced in Section 2.9. We use the same notation here, that is, $m(k)$ denotes the expected number of offspring per individual in the kth reproduction cycle.

5.10.1 Deterministically varying environments

In Section 2.9 it is shown that

$$\mathbb{E}[Z_n] = \prod_{k=0}^{n-1} m(k)\mathbb{E}[Z_0] \, . \tag{5.151}$$

As mentioned there, this result is true whether or not reproduction of different individuals is independent. For the results in this subsection and the next, however, the independence assumption is necessary.

The generating function of the offspring distribution of individuals in the kth generation is defined as

$$f(k,s) = \mathbb{E}[s^{\xi(k)}] = \sum_{j=0}^{\infty} \mathbb{P}(\xi(k) = j)s^j = \sum_{j=0}^{\infty} p_j(k)s^j \, , \tag{5.152}$$

with $0 \le s \le 1$, where $\xi(k)$ denotes the number of offspring of an individual of the kth generation, and $p_j(k)$ the chance that this equals j.

Furthermore, we define the generating function of the number of individuals of generation k in a population that consists of one individual in generation

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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.

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