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Bisexual Galton-Watson Processes: A Survey

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Bisexual Galton-Watson Processes: A Survey

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Model description and assumptions. Classical (simple) Galton-Watson processes (abbreviated as GWP hereafter) as well as their neighbours do not, at least not explicitly, distinguish between sexes of individuals. This means for the populations these processes describe that they are either assumed be asexual or that their male (nonreproductive) part is simply ignored. The latter can be overcome by using a 2-type GWP for which only type 1 individuals, the females, can produce offspring. However, such a model still ignores the fact that reproduction in two sex populations is based on the formation of couples, called *mating*. In the following we want to provide some insight in how mating may be incorporated into a branching model without moving too far from the paradigmatic assumptions GWP are built upon. This leads to the class of so-called *bisexual Galton-Watson processes (BGWP)*. We will focus on the problem of finding conditions for certain extinction, on a description of population growth on the event of nonextinction and, finally, on a comparison of extinction probabilities for certain mating types to the respective probabilities in the asexual case.

The fundamental contribution came in 1968, when Daley [6] introduced the following model: Consider a population whose 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, M_n are random variables and ζ is a deterministic function, called a *mating function*. Each couple produces offspring independently of all other couples and according to the same distribution $(p_{j,k})_{j,k\geq 0}$ on the set of pairs (j,k) of nonnegative integers. Hence for each couple $p_{j,k}$ denotes the probability of begetting j female and k male children. With $X_{n,k}$ and $Y_{n,k}$ denoting the number of female, respectively male offspring of the k-th couple of the n-th generation (labelled in arbitrary fashion), we arrive at the important recursive identities

$$F_{n+1} \;=\; \sum_{k=1}^{Z_n} X_{n,k} \quad\text{and}\quad M_{n+1} \;=\; \sum_{k=1}^{Z_n} Y_{n,k} \tag{1}$$

for $n \geq 0$, where the $(X_{n,k}, Y_{n,k})$ are independent and identically distributed according to $(p_{j,k})_{j,k\geq 0}$. This is the familiar structure for GWP 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 $\zeta(x,y) \overset{\text{def}}{=} x$ we see that Z_n just equals the number of females in the n-th generation ($Z_n = F_n$ for all $n \geq 0$) and is indeed a classical GWP. In the general model $(Z_n)_{n\geq 0}$ is called a *bisexual Galton-Watson process* with offspring distribution $(p_{j,k})_{j,k\geq 0}$ and mating function ζ. Like its classical counterpart, it forms a temporally homogeneous Markov chain on the nonnegative integers with transition probabilities

$$\mathbb{P}(Z_{n+1} = j | Z_n = i) \;=\; \mathbb{P}\Big(\zeta\big(\textstyle\sum_{k=1}^{i} X_{n+1,k}, \sum_{k=1}^{i} Y_{n+1,k}\big) = j\Big) \tag{2}$$

for all $i, j, n = 0, 1, 2, ...$ These do not depend on n because of the independence and identical distribution of the $(X_{n,k}, Y_{n,k})$ for all $k, n = 0, 1, 2, ...$

From a mathematical viewpoint it is desirable to restrict further the class of offspring distributions in order to facilitate more explicit computations. Daley [6] gave two alternative assumptions, at least the first of which being also reasonable from a biologist's perspective.

ASSUMPTION 1. Suppose that each couple begets children according to an offspring distribution $(\hat{p}_j)_{j\geq 0}$ and that, for each child, "god throws a θ-coin", $0 < \theta < 1$, to decide whether it is a female, which happens with probability θ, or a male. All coin tosses are, of course, independent of "the rest of the world", in particular independent of each other and of the total number of children of the considered couple.

ASSUMPTION 2. Suppose that the random numbers of female and male offspring for a couple are independent, that is, $X_{n,k}$ and $Y_{n,k}$ are independent for each $n \geq 0$ and $k \geq 1$ with distributions $(p_j^F)_{j\geq 0}$ and $(p_j^M)_{j\geq 0}$, say.

To see what these assumptions imply for the offspring distribution $(p_{j,k})_{j,k\geq 0}$, note that, under Assumption 1, $p_{j,k}$ denotes the probability that a couple begets $j+k$ children, which occurs with probability $\hat{p}_{j+k}$, and that in exactly j of the entailed $j+k$ θ-coin tosses "head" comes up, which happens with the binomial probability $\binom{j+k}{j}\theta^j(1-\theta)^k$. Consequently,

$$p_{j,k} \;=\; \binom{j+k}{j}\theta^j(1-\theta)^k\,\hat{p}_{j+k} \tag{3}$$

for all $j, k \geq 0$ (check that this is trivially correct if $j = k = 0$). Under Assumption 2, we immediately have by independence that

$$p_{j,k} \;=\; p_j^F p_k^M \tag{4}$$

for all $j, k \geq 0$. Equivalence of both assumptions can be easily verified if $(p_j^F)_{j\geq 0}$, $(p_j^M)_{j\geq 0}$ and $(\hat{p}_j)_{j\geq 0}$ are Poisson distributions with means m^F, m^M and $m^F + m^M$, respectively, and if $\theta = m^F/(m^F + m^G)$. Let us stipulate without further notice that hereafter $(p_{j,k})_{j,k\geq 0}$ always satisfies Assumption 1 or 2 and further

$$\beta \overset{\text{def}}{=} \max(p_{0,\bullet}, p_{\bullet,0}) > 0, \tag{5}$$

where $p_{0,\bullet} \overset{\text{def}}{=} \sum_{k\geq 0} p_{0,k}$ and $p_{\bullet,0} \overset{\text{def}}{=} \sum_{j\geq 0} p_{j,0}$ denote the respective probabilities, that a couple has only male or only female offspring. Condition (5) holds automatically under Assumption 1 because $0 < \theta < 1$, and is equivalent to $\max(p_0^F, p_0^M) > 0$ under Assumption 2.

So far no restrictions have been imposed on the mating function ζ which, as should be intuitively clear, constitutes an intrinsic parameter of the model in that the behaviour of the process $(Z_n)_{n\geq 0}$ highly depends on how ζ is chosen. The following is a list of some *common sense conditions* for ζ:

- A void generation cannot produce offspring, hence $\zeta(0,0) \overset{\text{def}}{=} 0$. Ruling out asexual reproduction, the same should hold whenever a generation contains no females or no males, i.e. $\zeta(x,y) = 0$ whenever $x = 0$ or $y = 0$.
- An increased number of females or males in a generation should never decrease the number of formed couples, so we assume ζ be nondecreasing in both arguments.
- If the numbers of both, females and males within a generation, increase to infinity, then so does the number of formed couples, formally expressed as $\lim_{x,y\to\infty} \zeta(x,y) = \infty$.

Hereafter, we call ζ a *common sense mating function* if it satisfies the previous conditions. Various more or less realistic common sense mating functions have been proposed in the literature [6], [7], [11]. We list here four of those which allow a good interpretation in terms of the general pattern of sexual interaction in the considered population (monogamy, polygamy, promiscuity).

- $\zeta(x,y) = \min(x,y)$ [monogamous mating, mating with perfect (mutual) fidelity];
- $\zeta(x,y) = \min(x,dy)$, $d \geq 2$ an integer [polygamous mating, men can have up to d spouses];
- $\zeta(x,y) = x\min(1,y)$ [(unilateral) promiscuous mating];
- $\zeta(x,y) = xy$ [(bilateral) promiscuous mating].

As monogamous and polygamous mating are frequently observed patterns in real world populations, the first two mating functions are of particular interest.

Towards a mathematical analysis of BGWP Hull [11] made the significant observation that the mating functions likely to occur in real-life models are *superadditive*, the formal definition being

$$\zeta(x_1 + x_2, y_1 + y_2) \;\geq\; \zeta(x_1, y_1) + \zeta(x_2, y_2)$$

for all $x_1, x_2, y_1, y_2 = 0, 1, 2, \ldots$ Intuitively speaking, this means that if we divide a two sex population with mating function ζ into two parts and allow mating only within the two subpopulations, then the total number of formed couples cannot be larger than in the case of no subdivision. Notice that all four mating functions above share this property.

Extinction. Let us briefly argue that the merciless dichotomy of extinction or explosion, that is

$$\mathbb{P}(Z_n = 0 \text{ eventually}|Z_0 = k) + \mathbb{P}(Z_n \to \infty|Z_0 = k) \; = \; 1 \quad \text{for all } k = 1, 2, ...$$

also holds for any BGWP with common sense mating function and satisfying our standing condition (5). Indeed, supposing the contrary, there must exist positive integers k, N such that

$$\gamma \; \overset{\text{def}}{=} \; \mathbb{P}(1 \le Z_n \le N \text{ for infinitely many } n \ge 0|Z_0 = k) \; > \; 0.$$

It may be argued on an intuitive level and actually turned into a metatheorem that this cannot hold for any proper population. Since for BGWP a rigorous argument is supplied rather easily we provide it here for the interested reader. Let $T_1, T_2, ...$ be the successive random times where the population size falls below N. Recalling that $(Z_n)_{n\ge0}$ is a temporally homogeneous Markov chain with 0 as an absorbing state, we infer with the help of the strong Markov property[1] and condition (5) that

$$\begin{aligned}
\gamma_{n+1} \; &\overset{\text{def}}{=} \; \mathbb{P}(1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m \le n+1|Z_0 = k) \\
&\le \; \mathbb{P}(Z_{T_{2n}+1} \ne 0, 1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m \le n|Z_0 = k) \\
&= \; \sum_{j=1}^{N} \mathbb{P}(Z_{T_{2n}+1} \ne 0|Z_{T_{2n}} = j)\mathbb{P}(Z_{T_{2n}} = j, 1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m < n|Z_0 = k) \\
&= \; \sum_{j=1}^{N} \mathbb{P}(Z_1 \ne 0|Z_0 = j)\mathbb{P}(Z_{T_{2n}} = j, 1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m < n|Z_0 = k) \\
&\le \; \sum_{j=1}^{N} (1 - p^{j}_{\bullet,0} - p^{j}_{0,\bullet})\mathbb{P}(Z_{T_{2n}} = j, 1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m < n|Z_0 = k) \\
&\le \; (1 - \beta^N)\mathbb{P}(1 \le Z_{T_{2m}} \le N \text{ for each } 1 \le m \le n|Z_0 = k) \\
&= \; (1 - \beta^N)\gamma_n \\
\le ... &\le (1 - \beta^N)^n \gamma_1
\end{aligned}$$

for all $n \ge 1$, which together with $\gamma_n \downarrow \gamma$ yields the contradiction via

$$0 \; < \; \gamma \; = \; \lim_{n\to\infty} \gamma_n \; \le \; \gamma_1 \lim_{n\to\infty} (1 - \beta^N)^{n-1} \; = \; 0.$$

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[1] This means that the Markov property remains valid if fixed time epochs are replaced with random times T having the *non-anticipation property*, i.e., for each $n \ge 0$, the event $\{T = n\}$ does only depend on $Z_0, ..., Z_n$ but not on $Z_{n+1}, Z_{n+2}, ...$ Such random times are called stopping times.

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

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

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 $Q_1 = Q_2 = ... = 1$? For the simple GWP with offspring distribution $(p_j)_{j\geq 0}$ and mean offspring $m = \sum_{j\geq 0} jp_j = \mathbb{E}[Z_1|Z_0 = 1]$ per individual the analysis reduces to a consideration of $Q = Q_1$, because $Q_j = Q^j$ for each $j \geq 1$, and the simple and very intuitive answer is that $Q = 1$ if, and only if, $m \leq 1$ and $p_0 > 0$. So certain extinction occurs if, and only if, each individual begets at most one child on the average and has a positive chance of having no children.

The following example due to Hull [11] shows that one cannot expect an equally simple answer for general BGWP. Consider the common sense, superadditive mating function ζ defined by $\zeta(x, y) \overset{\text{def}}{=} 0$, if $x = 0$ or $y = 0$, and $\zeta(x, y) \overset{\text{def}}{=} x + y - 1$, otherwise. Let the $p_{j,k}$ be of the form (3) 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 n-th generation produce only female or only male offspring. By comparison with a process of an inbreeding population where couples are formed only by children of the same parents, Hull could show that $Q_j < 1$ for all $j \geq 1$ and any choice of θ (see Theorem 1 and its proof below). On the other hand,

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

is strictly less than 1 if $\theta = 0.8$. However, as pointed out later by Bruss [5], one should rather look here at the *average unit reproduction means*

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

giving the mean population growth rates per generation for the various levels j. For the simple GWP this is disguised by the lucky coincidence that m_j does not depend on j. In the given example,

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

which, for any choice of θ, increases to 3 as j tends to infinity. In 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 where 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. [7] that this latter observation holds true more generally.

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

For those readers wondering whether there are examples of ultimately supercritical BGWP with common sense, superadditive mating functions which 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 a 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 $i \in I\!N$, then ultimate supercriticality implies a positive chance of survivial for *all* initial population sizes, so $i_0 = 1$ and $1 > Q_1 \geq Q_2 \geq ...$

By the strong law of large numbers, $\overline{X}_{1,j} \overset{\text{def}}{=} j^{-1}\sum_{i=1}^{j} X_{1,i}$ and $\overline{Y}_{1,j} \overset{\text{def}}{=} j^{-1}\sum_{i=1}^{j} Y_{1,i}$ tend to $m^F \overset{\text{def}}{=} \mathbb{E}[X_{1,1}]$ and $m^M \overset{\text{def}}{=} \mathbb{E}[Y_{1,1}]$, respectively, which are the average numbers of female and male children per couple. Writing

$$m_\infty \;=\; \lim_{j\to\infty} \mathbb{E}\big[\zeta\big(\textstyle\sum_{i=1}^{j} X_{1,i}, \sum_{i=1}^{j} Y_{1,i}\big)\big]/i \;=\; \lim_{j\to\infty} \mathbb{E}\big[\zeta\big(j\overline{X}_{1,j}, j\overline{X}_{1,j}\big)\big]/j,$$

it should not be surprising that one can show that

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

for a suitable function r (see [7, Lemma 2.3]). We note in passing the technical point that m^F, m^M need not be integers, but that, by linear interpolation, $\zeta(x,y)$ can always be defined for all pairs (x,y) of nonnegative numbers without losing superadditivity. For the four examples given above this is clear anyway. Although it may be generally hard to determine r explicitly, there are many examples of ζ including ours where this is easy. In fact,

- $\zeta(x,y) = \min(x, dy)$, $d \in I\!N$, implies $r = \zeta$ and $m_\infty = \min(m^F, dm^M)$;
- $\zeta(x,y) = x\min(1,y)$ implies $r(x,y) = x$ and $m_\infty = m^F$;
- $\zeta(x,y) = xy$ implies $r(x,y) = \infty$ for all x,y and $m_\infty = \infty$.

Proof of Theorem 1. In the following we present the main arguments to prove Theorem 1 but are leaving out any technicalities.

The first observation to make is that, by (2) and the monotonicity of the mating function

ζ in each argument,

$$\begin{aligned} \mathbb{P}(Z_1 > k|Z_0 = i) &= \mathbb{P}\Big(\zeta\big(\textstyle\sum_{j=1}^{i} X_{1,j}, \sum_{j=1}^{i} Y_{1,j}\big) > k\Big) \\ &\le \mathbb{P}\Big(\zeta\big(\textstyle\sum_{j=1}^{i+1} X_{1,j}, \sum_{j=1}^{i+1} Y_{1,j}\big) > k\Big) \\ &= \mathbb{P}(Z_1 > k|Z_0 = i+1) \end{aligned} \tag{6}$$

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 (6) generalises to

$$\mathbb{P}(Z_n > k|Z_0 = i) \;\le\; \mathbb{P}(Z_n > k|Z_0 = i+1) \tag{7}$$

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 (7),

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

for all $i \in I\!N_0$. Here is 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 $(Z_n')_{n\ge 0}$ the BGWP based on this subset, hence $Z_0' = i$. Then the Z_1 couples forming 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 due to the one additional ancestor couple in the original population and the monotonicity of the mating function. This shows $Z_1' \le Z_1$ and finally leads to the conclusion $Z_n' \le Z_n$ for all $n \ge 0$ when repeating the argument for the subsequent generations. Since the extinction probabilities of $(Z_n)_{n\ge 0}$ and $(Z_n')_{n\ge 0}$ are Q_{i+1} and Q_i, respectively, the inequality $Q_i \ge Q_{i+1}$ follows as a particular consequence.

The superadditivity of ζ has not yet entered into our arguments and is used next to infer the superadditivity of $jm_j = \mathbb{E}[Z_1|Z_0 = j]$ in j, defined by $(j+k)m_{j+k} \ge jm_j + km_k$ for all $j, k \ge 1$. Applying standard results on superadditive functions to $(jm_j)_{j\ge 1}$ (see e.g. [10]) then yields the asserted convergence of the m_j to $m_\infty = \sup_{k\ge 1} m_k$. Indeed,

$$\begin{aligned} (j+k)m_{j+k} &= \mathbb{E}[Z_1|Z_0 = j+k] \\ &= \mathbb{E}\Big[\zeta\big(\textstyle\sum_{l=1}^{j+k} X_{1,l}, \sum_{l=1}^{j+k} Y_{1,l}\big)\Big] \\ &\ge \mathbb{E}\Big[\zeta\big(\textstyle\sum_{l=1}^{j} X_{1,l}, \sum_{l=1}^{j} Y_{1,l}\big)\Big] + \mathbb{E}\Big[\zeta\big(\textstyle\sum_{l=j+1}^{j+k} X_{1,l}, \sum_{l=j+1}^{j+k} Y_{1,l}\big)\Big] \\ &= \mathbb{E}\Big[\zeta\big(\textstyle\sum_{l=1}^{j} X_{1,l}, \sum_{l=1}^{j} Y_{1,l}\big)\Big] + \mathbb{E}\Big[\zeta\big(\textstyle\sum_{l=1}^{k} X_{1,l}, \sum_{l=1}^{k} Y_{1,l}\big)\Big] \\ &= \mathbb{E}[Z_1|Z_0 = j] + \mathbb{E}[Z_1|Z_0 = k] \\ &= jm_j + km_k \end{aligned}$$

for all $j, k \ge 1$, where superadditivity of ζ has been utilised in the third line and further independence and identical distribution of the offspring variables $(X_{1,l}, Y_{1,l})$ in the fourth line.

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

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

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

To see that $Q_i < 1$ for all sufficiently large i in case $m_\infty > 1$ is more difficult and too technical for being presented here. However, a rather simple argument due to Hull [11] exists under the stronger condition $m_1 > 1$ and is again based on a comparison of $(Z_n)_{n\geq 0}$ with another process, in fact a supercritical simple GWP. Define $Z_0' \overset{\text{def}}{=} Z_0$ and then recursively

$$Z_n' \;\overset{\text{def}}{=}\; \sum_{j=1}^{Z_{n-1}'} \zeta(X_{n,j}, Y_{n,j})$$

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

$$Z_1' \;=\; \textstyle\sum_{j=1}^{Z_0} \zeta(X_{1,j}, Y_{1,j}) \;\leq\; \zeta\big(\sum_{j=1}^{Z_0} X_{1,j}, \sum_{j=1}^{Z_0} Y_{1,j}\big) \;=\; Z_1$$

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

Growth behaviour in case of survival. We stay with the ultimately supercritical case ($m_\infty > 1$) and take a look at the question how the considered population grows on the event of survival. Since m_∞ describes the asymptotic growth rate per generation if the population becomes large, it is not unreasonable to believe that Z_n grows like m_∞^n on the event of survival. On the other hand, even for the simple GWP the famous Kesten-Stigum theorem already taught us this be true only under an additional condition on the offspring distribution. Defining the normalised process

$$W_n \;\overset{\text{def}}{=}\; \frac{Z_n}{m_\infty^n}, \quad n \geq 0,$$

we have that

$$\begin{aligned}\mathbb{E}[W_{n+1}|W_n = im_\infty^{-n}] &= \mathbb{E}[W_{n+1}|Z_n = i] \\ &= m_\infty^{-(n+1)}\mathbb{E}[Z_{n+1}|Z_n = i] \\ &= im_i m_\infty^{-(n+1)} \\ &\leq im_\infty^{-n}\end{aligned} \tag{8}$$

for all i, whence $(W_n)_{n\geq 0}$ constitutes a nonnegative supermartingale and therefore converges to a finite random variable W with expectation $\mathbb{E}[W|Z_0 = i] \leq \mathbb{E}[W_0|Z_0 = i] = i$ for all i. In other words, the long run population growth rate is at most m_∞ which should not come by surprise because the average unit reproduction means are bounded by this value. But when is m_∞^n also the correct normalization in the sense that the limiting variable W is positive on the event of survival? The difficulty of this question is best understood when viewing the approximation of Z_n by Wm_∞^n as a two step result. Writing Z_n as the product $\frac{Z_n}{Z_{n-1}} \cdot \frac{Z_{n-1}}{Z_{n-2}} \cdot \ldots \cdot \frac{Z_1}{Z_0}$, replace first each factor $\frac{Z_k}{Z_{k-1}}$ with its conditional expectation given Z_{k-1}, that is $m_{Z_{k-1}}$, and then the latter with its limit (and upper bound) m_∞ as Z_{k-1} tends to infinity. This leads to the decomposition

$$W_n = V_n \cdot \prod_{k=0}^{n-1} \frac{m_{Z_k}}{m_\infty}, \tag{9}$$

where $V_0 \overset{\text{def}}{=} Z_0$ and

$$V_n \overset{\text{def}}{=} \frac{Z_n}{m_{Z_0} \cdot \ldots \cdot m_{Z_{n-1}}}, \quad n \geq 1.$$

A similar computation as in (8) shows that $(V_n)_{n\geq 0}$ constitutes a nonnegative martingale, i.e. $\mathbb{E}[V_{n+1}|V_n = v] = v$ for all n and v, and hence converges to a random variable V which is $\geq W$ because $V_n \geq W_n$ for all n. Taking limits in (9) now yields that

$$W = V \cdot \prod_{k\geq 0} \frac{m_{Z_k}}{m_\infty}.$$

So Z_n grows indeed like m_∞^n on the event of survival if the martingale limit V as well as the infinite product $\prod_{k\geq 0} \frac{m_{Z_k}}{m_\infty}$ are positive on that event, where the latter obviously holds true if m_j converges to m_∞ sufficiently fast. However, without a restriction to special mating functions it seems difficult to translate these requirements into conditions on the model parameter $(p_{j,k})_{j,k\geq 0}$. Gonzales and Molina [8], [9] did some related work for general ζ but circumvented the problem by directly imposing conditions on the *derived* quantities $d_j \overset{\text{def}}{=} m_j - m_\infty$, an essential one being that $d_j \leq g(j)$ for all j and a suitable concave function g satisfying $\sum_{j\geq 1} j^{-1}g(j) < \infty$. By adding further conditions not reported here they could prove that Z_n grows like m_∞^n (W is positive) on an event of positive probability, but not necessarily the full event of survival.

At least for monogamous populations with mating function $\zeta(x, y) = \min(x, y)$, Bagley [3] was able to provide a satisfactory answer, Theorem 2 below, which is actually the perfect analogue of the corresponding result for asexual populations described by simple GWP. Recall that p_j^F and p_k^M denote the probabilities that a couple has exactly j female, respectively k male offspring, hence $p_j^F = \sum_{k\ge 0} p_{j,k}$ and $p_k^M = \sum_{j\ge 0} p_{j,k}$.

THEOREM 2. *Let $(Z_n)_{n\ge 0}$ be an ultimately supercritical BGWP with monogamous mating function ζ and offspring distribution $(p_{j,k})_{j,k\ge 0}$ satisfying Assumption 1. Then $\sum_{k\ge 1} p_k^F k\log k < \infty$ implies that W is positive on the event of survival, i.e. $\mathbb{P}(W>0|Z_0=i) = 1-Q_i$ for all i, while $\sum_{k\ge 1} p_k^F k\log k = \infty$ implies $W=0$.*

As one can easily verify, $\sum_{k\ge 1} p_k^F k\log k < \infty$ and $\sum_{k\ge 1} p_k^M k\log k < \infty$ are equivalent conditions under Assumption 1 because $0<\theta<1$.

SKETCH OF PROOF. We will content ourselves with the following very intuitive heuristic argument under the additional assumption $m^F \ne m^M$ or, equivalently, $\theta \ne \frac{1}{2}$. To be specific suppose $m^F < m^M$. If the population survives and hence grows to infinity then eventually the total number of female offspring produced by a generation is always smaller than the respective number of male offspring. In fact, the law of large numbers even tells us that

$$\frac{1}{Z_n}(M_{n+1} - F_{n+1}) \;=\; \frac{1}{Z_n}\sum_{k=1}^{Z_n}(Y_{n+1,k} - X_{n+1,k})$$

tends to $m^M - m^F > 0$, if $Z_n \to \infty$. Consequently, for large n the number of couples forming the $(n+1)$-st generation just equals the number of female offspring of the previous one, whence $(Z_n)_{n\ge 0}$ ultimately behaves like the simple GWP obtained by only looking at the females. The assertions of the theorem now follow by invoking the Kesten-Stigum theorem.

It is quite clear that the heuristic just given remains true if the offspring distribution satisfies Assumption 2. Since $m_\infty = \min(m^F, m^G)$, Theorem 2 shows, even if $m^F = m^M$, that a surviving monogamous population grows at the same order of magnitude as one of its associated asexual counterparts in which females, respectively males reproduce without mating. Of course, the probability of survival is always smaller in the bisexual case. The same heuristic becomes exact for (unilateral) promiscuous populations because in case of survival the number of couples precisely equals the number of females in each generation. The male subpopulation enters into the analysis only by causing an increased chance of extinction.

Bisexual versus asexual branching: 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 serve as an explanation that only very few related contributions are found in the literature, namely [7], [1] and [2]. For the classical GWP, the extinction probability Q_i given 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 fixed point equation $f(s) = s$

where $f(s) = \sum_{j\geq 0} p_j s^j$ denotes the generating function of the offspring distribution $(p_j)_{j\geq 0}$. Unfortunately, there is no such simple way to compute Q_i for BGWP however the mating function is chosen.

Daley et al. [7] suggest a finite Markov chain approximation which is roughly described as follows: Let $(Z_n)_{n\geq 0}$ be any BGWP with superadditive mating function ζ and recall that $(Z_n)_{n\geq 0}$ forms a temporally homogeneous Markov chain with transition matrix $P = (P_{ij})_{i,j\geq 0}$, i.e.

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

denotes the conditional probability that, at any time $n = 0, 1, 2, ...$, 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 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 like $(Z_n)_{n\geq 0}$ 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. On the other hand, 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

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

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

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

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

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

which in matrix form reads

$$\boldsymbol{Q}(N) \;=\; (\boldsymbol{I} - \boldsymbol{R}(N))^{-1} \boldsymbol{P}_0(N),$$

where

$$\boldsymbol{Q}(N) \overset{\text{def}}{=} \begin{pmatrix} Q_1(N) \\ \vdots \\ Q_N(N) \end{pmatrix}, \quad \boldsymbol{P}_0(N) \overset{\text{def}}{=} \begin{pmatrix} P_{10} \\ \vdots \\ P_{N0} \end{pmatrix}, \quad \boldsymbol{R}(N) \overset{\text{def}}{=} \begin{pmatrix} P_{11} & \dots & P_{1N} \\ \vdots & \ddots & \\ P_{N1} & \dots & P_{NN} \end{pmatrix}$$

and $\boldsymbol{I}$ is the identity matrix. Note that $(\boldsymbol{I}-\boldsymbol{R}(N))^{-1} = \boldsymbol{I}+\boldsymbol{R}(N)+\boldsymbol{R}(N)^2+...$ The following result from [7] provides an estimate for $Q_i - Q_i(N)$ for $N \geq i$ and is stated without proof.

Theorem 3. *Given a BGWP $(Z_n)_{n\geq 0}$ with superadditive mating function,*

$$Q_i(i+j-1) \;\leq\; Q_i \;\leq\; \min\left(1, \frac{Q_i(i+j-1)}{1-Q_j(i+j-1)}\right) \tag{10}$$

for all $i, j \geq 1$.

Daley et al. used this finite chain approximation to compute the extinction probabilities Q_i of supercritical BGWP with monogamous or (unilateral) promiscuous mating function for various initial generation sizes i. The numbers of female and male offspring per individual were assumed to be independent (Assumption 2) with a Poisson distribution with mean 1.2, i.e.

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

The simple (asexual) GWP 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 BGWP which are clearly larger. Based upon the numbers in [7], the following table shows the values of the extinction probability ratio $R_i \overset{\text{def}}{=} Q_i/0.6863^i$ for various initial generation sizes i.

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

In the monogamous case R_i apparently tends to infinity. Daley et al. note that there does not appear to be a simple way to find the precise asymptotic behaviour 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 rapidly converge to about 1.33, however without having a theoretical explanation for the particular value. On the other hand, convergence of R_i is quite plausible in view of the fact that the promiscuous BGWP behaves exactly like the simple GWP pertaining to the female subpopulation as long as at least one male is born in each generation. An additional chance of extinction is only caused by the chance 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 [1] and [2] provide a deeper analysis of promiscuous BGWP with offspring distributions satisfying Assumption 2. Although the mathematical details are far beyond the scope of this survey as involving potential theoretic aspects of GWP, we summarize the major findings from there in the Theorem 4 below.

So we consider a (unilateral) promiscuous BGWP $(Z_n)_{n\geq 0}$ with probabilities $p_{j,k} = p_j^F p_k^M$ of having j daughters and k sons per couple (see (4)). Since Z_n equals the number of females in the n-th generation as long as at least one male is alive (but regardless how many) it follows easily with Assumption 2 that the extinction probabilities Q_i depend on $(p_k^M)_{k\geq 0}$ only through $\kappa \overset{\text{def}}{=} p_0^M$, the probability that a couple has no male offspring. Let $f(s) = \sum_{j\geq 0} p_j^F s^j$ be the generating function of the female offspring distribution $(p_j^F)_{j\geq 0}$, f_n its n-th iterate and Q the extinction probability of the associated simple GWP $(F_n)_{n\geq 0}$, say, with this offspring distribution. Hence Q is the smallest fixed point of f in $[0, 1]$, and $f_n(s) \uparrow Q$ for each $s \leq Q$.

THEOREM 4. *Suppose that* $m^F = \sum_{j\geq 1} jp_j^F > 1$ *and* $\kappa < 1$.

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

(i) If $\kappa < p_0^F$ *then*

$$1 \;\leq\; R_i \;\leq\; 1 + \frac{\kappa}{p_0^F}. \tag{11}$$

(ii) If $\kappa = p_0^F$ *then*

$$1 + \frac{1-Q}{1+Q-p_0^F} \;\leq\; R_i \;\leq\; 2 \tag{12}$$

(iii) If $p_0^F < \kappa < Q$ *then*

$$1 + \frac{\kappa(1-Q)}{\kappa Q + (1-\kappa)p_0^F} \;\leq\; R_i \;\leq\; (n+2)\left(\frac{1}{1-\kappa} + \frac{p_0^F}{\kappa}\right) \tag{13}$$

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

(iv) If $\kappa = Q$ *then*

$$\frac{1-Q}{Q(a_1-Q)+(1-Q)} \;\leq\; \frac{R_i}{a_i} \;\leq\; \frac{1}{1-q} + \frac{p_0}{q} \tag{14}$$

where $a_i \overset{\text{def}}{=} \mathbb{E}(\tau | \tau < \infty, F_0 = i)$, $\tau = \inf\{n \geq 0 : F_n = 0\}$.

(v) If $\kappa > q$ then

$$1 \;\le\; \frac{Q_i}{\kappa^i} \;\le\; 1 + \frac{f(\kappa)}{\kappa - f(\kappa)}. \tag{15}$$

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

$$\lim_{i\to\infty} \log\left(\frac{1}{f'(Q)}\right)\frac{R_i}{a_i} \;=\; \lim_{i\to\infty} \frac{R_i}{\log i} \;=\; 1 \tag{16}$$

if $\kappa = Q$, and

$$\lim_{i\to\infty} \frac{R_i}{\kappa^i} \;=\; 1 \tag{17}$$

if $\kappa > Q$.

The most intriguing result stated in Theorem 4 is that for $0 < \kappa < Q$ convergence of R_i fails to hold in general. This is even more surprising when noting 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., see [1] 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 [4]. It means that a considered sequence is seemingly convergent but in fact oscillating in a very small range (of the order 10^{-4} or smaller). The convergence results (16) and (17) are much more appealing to intuitive thinking, their interpretation being that for $\kappa \ge Q$ extinction of a population with large initial size is more likely to be caused by the disappearance of males than of females.

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