Figure 2.9 Alternative representations of a process with sibling dependence.

of its members. The process of these macro-individuals has independently reproducing elements, as different sibships are independent of each other. The numbers of "macro children" need, however, not be distributed identically (e.g., we might expect a large sibship to give birth to more children than a small one). Thus the macro-process is a multi-type branching process, and in the Galton–Watson case simply has sibship size as its type.

Example 2.10 Imagine a cell population in which if one cell divides, her sister cell cannot, but dies without trace. Then each individual (= cell) can produce zero or two children, but not independently. The two possibilities are that one sister cell divides, say with probability p, or that none does. The population of sibling pairs is again a single-type process, which produces one child (= pair) with probability p, and none with probability $1 - p$. If there are no dependences beyond that between sisters, the process of sister pairs is a classic independently reproducing branching process. This is illustrated in Figure 2.9.

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2.8 Sexual Reproduction

G. Alsmeyer

Up to now we have ignored that in species with sexual reproduction changes in population size depend on the formation of couples. Sometimes this may be justified. For instance, if mating is polygynous (one male may have many females), and the number of males is sufficiently large, the total number of females in a generation determines future population size. Another example is the number of initially rare mutants in an evolutionary process, for which, provided the residence

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population is large enough, pair formation is not a limiting factor. In many instances, however, mating is an important factor that cannot be dismissed. Bisexual Galton–Watson processes take mating into account explicitly. Unfortunately, this complicates life considerably, and few mathematical results are available.

So-called *bisexual* branching processes – a somewhat unfortunate name for processes with mating – were introduced by Daley (1968). In them it is convenient to represent population size by the *number of couples* rather than the number of individuals. Denote the number of couples in the nth generation by Z_n. The process starts with an initial number of couples, Z_0, just before the first reproduction period. Each couple has random numbers of female and male offspring. Thus, the offspring of a couple is represented by a pair of numbers, which are independently distributed for different couples, with an identical distribution that is constant over generations. In the simplest case it is assumed that, conditional on the total number of offspring, the offspring sex is determined at random (like flipping a, possibly biased, coin). Another model of sex determination assumes that the numbers of male and female offspring are independent with a possibly different distribution. The two mechanisms are equivalent for Poisson-distributed numbers of male and female offspring, since the sum of two independent Poisson variables is Poisson again. As in the Galton–Watson process, generations are non-overlapping.

The most realistic scenario is to form pairs according to a stochastic process. In existing theory, however, pair formation is assumed to be deterministic. Thus, the formation of couples is determined by a *mating function* $\zeta(x, y)$, which specifies the total number of couples formed if there are x females and y males. If mating is strictly monogamous and if we assume that the population is well-mixed, so that all possible pairs are formed, $\zeta(x, y)$ equals the minimum of x and y. In a polygynous mating system, in which each male may inseminate up to d females, $\zeta(x, y)$ is equal to the minimum of x and dy. Another, less common example, is unilateral promiscuous mating, where $\zeta(x, y)$ equals x times $\min(1, y)$. All these examples belong to the class of so-called *common sense mating functions*, which satisfy three natural conditions, i.e., a void generation cannot produce offspring, the number of couples increases with the numbers of males and females, and if the numbers of males and females tend to infinity so does the number of couples. Furthermore, these functions are *super-additive* (Hull 1982), which means that for all $x_1, x_2, y_1, y_2 = 0, 1, 2, \ldots$

$$\zeta(x_1 + x_2, y_1 + y_2) \geq \zeta(x_1, y_1) + \zeta(x_2, y_2) \,. \tag{2.77}$$

Super-additivity of the mating function implies that, if the population is divided into two subgroups that each form couples, the total number of couples is at most equal to that of the undivided population.

Common sense mating functions do not always make biological sense. As an example, consider the function $\zeta(x, y) = xy$, which could be called bilateral promiscuous mating. This function is unrealistic whenever there are more than just a few males: it implies that the total expected number of offspring per female increases linearly with the number of males in the population, since each female mates with every male and the numbers of offspring produced per couple (i.e., mating) are independent.

We number the couples in the nth generation in an arbitrary way and let X_k and Y_k denote the numbers of female and male offspring, respectively, of the kth couple. Conditionally, on the number of couples in the $(n-1)$th generation, Z_{n-1}, the number of couples in the next generation equals

$$Z_n = \zeta(\sum_{k=1}^{Z_{n-1}} X_k, \sum_{k=1}^{Z_{n-1}} Y_k) \ . \tag{2.78}$$

A process is extinct when Z_n equals zero. Bruss (1984) pointed out that the growth of a population is determined by the "average unit reproduction means"

$$m_j = \frac{1}{j}\mathbb{E}\left[Z_n \mid Z_{n-1} = j\right], \ j \geq 1 \ . \tag{2.79}$$

(Note that, in the standard Galton–Watson process, the expectation equals j times m, so m_j equals m.) Daley *et al.* (1986) showed that for common sense, superadditive mating functions, as j tends to infinity, m_j converges to a limit m_∞ with $m_j \leq m_\infty$ for all j, and that extinction is certain (irrespective of the initial population size) if this number is less than or equal to one. If $m_\infty > 1$, there is a positive survival probability provided the initial population size is large enough. If, however, the mating function and reproduction functions are such that, for all i,

$$\mathbb{P}\left(Z_n > i \mid Z_{n-1} = i\right) > 0 \ , \tag{2.80}$$

then $m_\infty > 1$ implies a positive survival probability for any initial positive population size.

From the above we can conclude

$$\mathbb{E}\left[Z_n \mid Z_{n-1}\right] = m_{Z_{n-1}} Z_{n-1} \leq m_\infty Z_{n-1} \ , \tag{2.81}$$

and then

$$\mathbb{E}\left[Z_n\right] \leq m_\infty \mathbb{E}\left[Z_{n-1}\right] \leq \cdots \leq m_\infty^n \mathbb{E}\left[Z_0\right] \ . \tag{2.82}$$

Thus, the expected population size does not necessarily change exponentially, as in the asexual branching process models already considered. Instead, decline may be more rapid if $m_\infty \leq 1$, and growth may be slower in the case of $m_\infty > 1$. The growth rate depends on characteristics of the mating function and offspring distributions. In Section 6.6 we examine population growth of these processes in more detail.

Example 2.11 Consider a small population of swans. Since these birds are strictly monogamous, we can use a model with mating function $\zeta(x, y) = \min(x, y)$. We assume that each couple has a chance $1 - q$ of producing zero offspring and a chance q of producing three surviving offspring. Given that a couple has offspring, the number of females is distributed Bin(3, p), with $p = 0.5$. Denote by $\mathbb{P}(x, y|j)$ the conditional probability that, given the adult population size equals j, the total number of female offspring equals x and the total

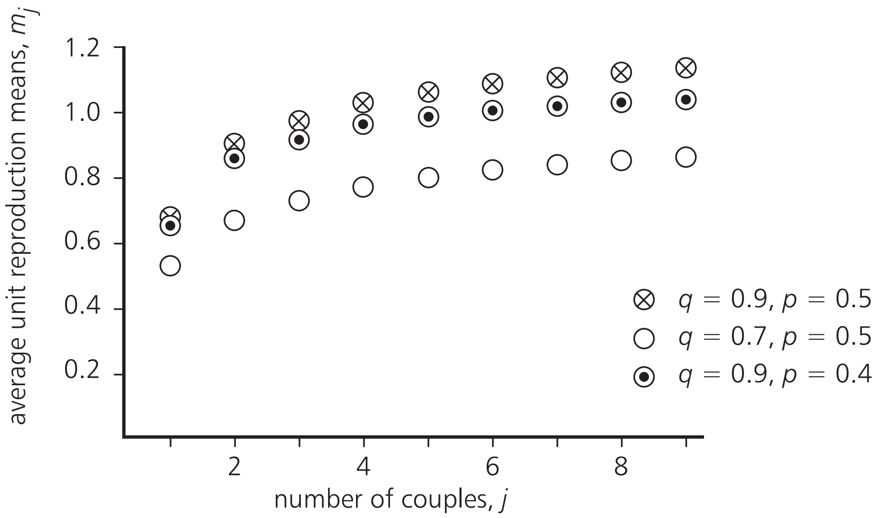

Figure 2.10 Values of m_j for the model given in Example 2.11, with different parameter values.

number of males equals y. Then

$$\mathbb{E}\left[\min(X,Y) \mid j\right] = \sum_{k=1}^{3j} \mathbb{P}\left(\min(X,Y) \geq k \mid j\right) = \sum_{k=1}^{3j} \sum_{x=k}^{3j} \sum_{y=k}^{3j} \mathbb{P}(x,y \mid j) \ , \tag{2.83}$$

since $\mathbb{E}[X] = \sum_{k\geq 1} \mathbb{P}(X \geq k)$ (see the Appendix). The probabilities $\mathbb{P}(x, y|j)$ can best be derived using probability generating functions (see the Appendix and Section 5.3). We used Mathematica to do these rather tedious calculations. Figure 2.10 shows m_j as a function of j for two different values of q. When q equals 0.7, m_∞ is about 0.85, so the population certainly becomes extinct. The expected number of offspring per couple is 2.1 in this case, so the expected number of offspring per individual equals 1.05 and an asexual branching process with this value of m would have a positive survival probability. When q equals 0.9, m_∞ equals approximately 1.1 and, accordingly, there is a positive chance that the population will persist. The survival probability of the population also depends on the proportion of females that is produced. When the chance of female offspring is not 1/2, the value of m_∞ drops, since the number of pairs that can be formed becomes lower. As shown in Figure 2.10, when $q = 0.9$ the process becomes nearly critical when the chance of having daughters, p, is 0.4 rather than 0.5. This illustrates that in sexually reproducing species, not only are the expected numbers of individuals important, but also their sex ratio is a critical factor in determining extinction probability. Obviously, this also depends on the mating system. When there is (slight) polygyny, for instance, we can expect that female-biased sex ratios are less risky than male-biased ones. The magnitude of such effects may be studied with bisexual branching process models. Extinction risks of processes with sexual reproduction are further discussed in Section 5.9.

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2.9 Varying Environments

The simple Galton–Watson processes, discussed in Section 2.1, give a general impression of what kind of phenomena branching models can elucidate. However,

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.

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