The Ancestral Pedigree of a Branching Process

R. B. Campbell

Department of Mathematics

University of Northern Iowa

Cedar Falls IA 50614-0506

campbell@math.uni.edu

http://www.math.uni.edu/∼campbell

(319) 273-2447

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ABSTRACT

A logistic (regulated population size) branching process is presented, and compared to a regular branching process and the Wright-Fisher model for properties including the coalescent time and the shape of the coalescent process. The similarity of these properties for the logistic branching process and the Wright-Fisher and regular banching process models indicates that these models are reasonable approximations for each other. In particular, the branching process is a reasonable approximation for the Wright-Fisher model even when alleles are not rare. The shape of the coalescent process (i.e., ancestral pedigree) confirms that most mutations should be of recent origin, hence rare. Whether the logistic branching process (or even an unconstrained branching process) is a more realistic model than the Wright- Fisher model is not discussed.

Introduction

Most of the theoretical work in population genetics is based on the Wright-Fisher Model (Ewens 1979). In particular, the diffusion approximation of Kimura (1962) and the coalescent analysis of Kingman (1980a,b) are based on it. Hence it is the model for which fixation and coalescent times have been calculated. (Actually the diffusion and coalescent analyses are based on a continuous approximation to the discrete Wright-Fisher model; the birth and death process is the continuous analog to the branching process discussed below.)

The Wright-Fisher model entails a constant population size and binomial progeny distribution. The assumption of constant population size is supported by the fact that population size is regulated by external resources; yet population size does fluctuate, in part because individuals cannot anticipate what other individuals will do. Hence the Wright-Fisher model may not be an appropriate model for natural populations.

Fisher (1922) introduced a branching process model with a Poisson progeny distribution, and Haldane (1927) used it to derive the now classical formula for the probability of fixation of a new advantageous mutation ($2s$). That result has been generalized, including an extension to fluctuating population size by Otto and Whitlock (1997). Another application of the model is the study of the probability of extinction of surnames (Hull 1998). Branching processes have also been used to study the coalescence of rare alleles (Rannala 1997). Another context in which branching processes have been used is to model the spread of mutations in geographically structured populations (Crump and Gillespie 1977, Sawyer 1979).

However, a branching process entails great fluctuations in population size (of the order

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of $\sqrt{N}$ each generation, where N is the population size). Especially since this variation cumulates over generations, this may entail greater fluctuation than occurs in nature. The branching process has mainly been used to model rare alleles, because in that context it has little impact on the total population size and is a good approximation to the Wright-Fisher model.

This manuscript will first present (review) the probability of fixation, expected time until fixation, and shape of the ancestral pedigree (coalescent process) for the Wright-Fisher model and the neutral branching process. A logistic (regulated) branching process will then be presented, and its similarity to the previous models with respect to fixation probability, expected time until fixation, and shape of the ancestral pedigree will be studied. A brief discussion of the impact of selection will follow.

Fixation Probability

The probability of fixation of a selectively neutral mutation is $1/N$ for a population of N individuals ($1/(2N)$ for a diploid population) by symmetry, hence this result merely merits mention. (Indeed, it must be shown that one of the alleles will become fixed.) However, an alternative proof for the branching process lays a foundation for expected time until fixation, hence is presented here.

The branching process model starts with a population of N distinct individuals (i.e., a haploid population is assumed; for comparison with diploid results replace N with $2N$), each of which independently reproduces with a Poisson progeny distribution with parameter one. Generations are discrete, hence the population contains N synchronized branching processes.

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The population will go extinct with probability one, but the expected time until extinction is infinite (Karlin and Taylor 1975).

Fixation shall be defined as when exactly one of the original N branching processes remains. It is possible that the last two (or more) remaining branching processes will go extinct the same generation, hence such fixation will not occur; but that will have very small probability, and we may ignore it.

To calculate the probability of fixation, let $p(t)$ be the probability that a branching process is extinct at time t, given that there was a single individual at time 1. Then if there were initially N individuals, the probability that exactly one lineage (i.e., descendants of one of those individuals) remains at time t is $(1 - p(t))(p(t))^{N-1}$ by independence. This expression is for a predesignated original individual, hence the probability that any one of the original individuals remains (with the other lineages extinct) is $N(1 - p(t))(p(t))^{N-1}$ since the events of different individuals remaining are mutually exclusive. The probability that a specified individual is the one which becomes fixed is given by $\int_1^\infty (1-p)(N-1)p^{N-2}dp/dt\, dt = \int_0^1 (1-p)(N-1)p^{N-2}dp = 1/N$, which, as noted above, is what symmetry requires if fixation eventually occurs since there are N original individuals. This has obviously entailed approximating a discrete branching process by a continuous one in order to take the derivative. Only the second half of the product rule for the derivative of the probability of one type being present $(d((1 - p(t))(p(t))^{N-1})/dt)$ was used because $-(p(t))^{N-1}dp/dt$ reflects the remaining lineage, hence entire population, going extinct; while $(1-p)(N-1)p^{N-2}dp/dt$ reflects other lineages going extinct so the designated one remains

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alone.

Expected Time until Fixation

The expected time until fixation for the Wright-Fisher model is a classic result from the diffusion approximation (Crow and Kimura 1970), and has also been calculated as the Coalescent time (Kingman 1982a,b), which is equal to the fixation time (Campbell 1999); the expected time until fixation is $2N$ generations. For the branching process model, employing the above notation, the expected time until fixation is given by $\int_1^\infty t(1-p)(N-1)p^{N-2}dp/dt\ dt$, which is intractable unless $p(t)$ is known. For the Poisson progeny distribution, it is known that $p(t) \doteq 1 - 2/t$ asymptotically (Holte 1974), and numerical evaluation of the composition of the generating function e^{s-1} evaluated at $s=0$ confirms that this approximation is good for $t > 20$. The integration for $t < 20$ will be small (assuming N is reasonably large) because p is small there, hence unimportant for the entire integral (dp/dt will not be large anywhere). Substituting $2/t$ for $1-p$ in the integral cancels out the factor of t and leaves $\int_1^\infty 2(N-1)p^{N-2}(dp/dt)dt = \int_0^1 2(N-1)p^{N-2}dp = 2$; this must be multiplied by N because there are N original genes which could become fixed. Hence the time until fixation is $2N$ generations. (This time would be $4N$ for a diploid model.)

For this neutral branching process model (Poisson progeny distribution) the population size will fluctuate by about $\sqrt{N}$ (where N is $N(t)$, not the original population size) each generation, because the variance for each individual is 1, and the variance of the sum is the sum of the variances. But the time until fixation is based upon the initial population size.

The Shape of the Ancestral Pedigree

The question is: what is the ancestral pedigree for a population? That is, what remains of the history of the population after all the lineages which have terminated have been removed. Ancestral pedigree and coalescent shall be used interchangeably to refer to all ancestors of the present population. Ancestral lineage shall refer to the set of unique individuals in each generation whose descendants will eventually become the population, i.e., the set of common ancestors of future populations; it is a lineage with one member each generation. We shall first consider the branching process model, and then extend the result to the Wright-Fisher model.

A Poisson progeny distribution with parameter 1 is assumed, but the important essence of that assumption is that the mean number of progeny is one and there is variance in the progeny distribution, so that all lineages (branching processes) will terminate with probability one. We are also assuming that the population is large, which entails that the branching process has been in existence for a long time.

Result I: If the number of individuals in the branching process is large, with high probability the original branching in the ancestral pedigree (in fact, all except recent branchings) is a bifurcation.

Note that this is not claiming that the original individual in the branching process split into two individuals, and neither lineage has gone extinct. The original individual could have had only one descendent, or several, all but one of whose lineages went extinct. Hence the pedigree may have several generations of one individual prior to the original individual which bifurcates. This is a statement about the most recent common ancestor, which might

have occurred several or many generations after the branching process was originated. Nor is this claiming that the most recent common ancestor had only two progeny, rather that the lineages from all but two of the progeny have gone extinct.

The essence of the proof is that when looking for the most recent common ancestor, you are looking for an individual with at least two descendent lineages surviving. Because lineages become extinct, it is unlikely that any more than the minimum number required to be a most recent common ancestor (2) will have survived.

For a more detailed proof, first assume that the progeny distribution (including those progeny whose lineages have gone extinct, not just progeny which are in the ancestral pedigree) along the ancestral lineage is not Poisson, but Poisson weighted by the number of progeny (which is the Poisson probability of one fewer progeny; i.e., the distribution of the number of sibs along the ancestral lineage is Poisson). This is the progeny distribution conditioned on that the lineage continues indefinitely. This provides an expected growth in the branching process of one individual per generation, which is greater than the growth rate of .5 individual per generation which actually occurs (.5 individuals per generation follows from the expected time until fixation being $2N$). The discrepancy is due to the fact that a branching process does not last for ever, but goes extinct with probability one. But a branching process which remains forever is a good model for getting a progeny distribution. Furthermore, The analysis is facilitated by the fact that a branching process which remains forever has probability 0, hence conditioning on it does not affect the other branches since they are missing a set of probability 0.

The size of a branching process (conditioned on not going extinct) grows linearly with time, which provides a triangular shape to the branching process. But the ancestral pedigree has many individuals (which are on lineages which have terminated, hence no members of the current generation are eliminated) removed from the branching process, which provides that the sides of the "triangle" for the ancestral pedigree will be concave. In fact, initial growth is very slow, with a great flourish at the end, perhaps resembling the shape of a golf tee.

Proof of Result I: Starting at time zero, ascend the ancestral lineage (set of common ancestors of future populations) until one or more siblings of the member of the ancestral lineage have descendent lineage(s) which survive until time t (the present). We are interested in the first time this occurs (which we shall denote as t_0). The lineages from siblings in previous generations will have terminated by time t (the present), and the parents of subsequent such siblings will not be common ancestors because there will be descendants of the sibling(s) at time t_0.

We are conditioning on that the ancestral lineage survives to time t (the present), and beyond, but the other lineages behave independently. The probability that an individual at time t_0 has descendants at time t is approximately $2/(t - t_0)$ for $t - t_0$ large, hence by independence the probability that two (specified) lineages both have descendants is $(2/(t - t_0))^2$, which is much smaller. Using the Poisson distribution for the number of sibs of the member of the ancestral lineage, and weighting by the probabilities of one or more of those sibs having descendants, it is readily verified that with high probability only one sibling will

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have descendants. Hence with high probability the original split in the ancestral pedigree will be a bifurcation.

The critical assumption in the above proof is that $t - t_0$ is large. Thus the same argument holds for subsequent branching in the ancestral pedigree as long as the time before the present is large. Essentially all early branchings in the ancestral pedigree will be bifurcations.

Result II: Most of the population is a result of recent branching, the ancestral pedigree is rather sparse if one goes back several generations. A branching process grows (approximately) linearly with t, but most of the early individuals are not in the pedigree of the current generation.

Proof of Result II: From the Poisson distribution, which has the probability of having no progeny equal to $1/e$, it is immediate that only $1 - 1/e$ of the previous generation contributed to the current generation, i.e., is part of the pedigree. Going back another generation, we are only interested in those individuals which contributed to the pedigree, so instead of $1 - 1/e$ we are interested in $1 - (1/e)^{(1-1/e)}$, which is the result of composing the generating function and subtracting from 1; two generations ago, the size of the ancestral pool is about 47% of the current population size. This is the probability of having descendants after the specified number of generations, composition of the generating function gives the probability of extinction. Composition of the generating function is soon approximated by the asymptotic result that $2/t$ of the population t generations ago has descendants in the present generation (because a branching process may fluctuate in size with time, this result is stated in terms of the population size t generations ago).

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If one is using the Wright-Fisher model with constant population size and binomial (multinomial) progeny distribution, the same result obtains. If the population size is N, the probability that an individual in the previous generation does not have a descendant in the present generation is $((N - 1)/N)^N$ which is equal to $(1/(1 + 1/(N - 1)))^N$ which is approximately $1/e$ for large N. The extension to more generations follows *mutatis mutandis*.

The approximation $2/t$ for the relative size of the pedigree t generations ago is a good approximation for $t > 20$. This provides, for example, that the pedigree size $\sqrt{2N}$ generations ago is approximately $N \times 2/\sqrt{2N} = \sqrt{2N}$. In particular, for a population of size 1000 (with expected time since a common ancestor equal to 2000), the expected size of the pedigree 45 generations ago is 45. If $N = 1\,000\,000$ (with expected time since a common ancestor equal to $2\,000\,000$), the expected size of the pedigree 1414 generations ago is 1414.

Similar results can be obtained with the coalescent analysis of Kingman (1982a, 1982b). The term $k(k - 1)/2$ which governs frequency of branching in the analysis of the coalescent confirms more growth in the recent pedigree (when k is large), but difficulty specifying initial conditions precludes an explicit solution for that model, and the exact structure may be different. Of course, there are large variances to all the results.

The shape of the ancestral pedigree (coalescent) can be obtained by combining the asymptotic result that the fraction of the population which persists for t generations is $2/t$ with numerical calculations for small t where that approximation is not reasonable. In particular, this answers the question of the distribution of when mutations in the population occurred, since the number of individuals in the ancestral pedigree as a function of the number of

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generations ago gives the relative frequency of when mutations occurred. Integration of $2/t$ for the $2N$ generations since the most recent common ancestor provides that the total number of individuals in the ancestral pedigree since the most recent common ancestor is approximately $2N\ln(2N)$. Explicit calculations for the 20 most recent generations when $2/t$ is not a good approximation for the ancestral pedigree size provides the better estimate $2N(\ln(2N) - .5)$ for the total size of the ancestral pedigree. To be specific, assuming $N = 1000$ (with the expected time since a common ancestor of 2000 generations) provides that $1/2$ of the individuals in the pedigree lived, hence $1/2$ of the allelic forms originated, in the most recent 35 generations; 90% of the individuals lived, hence 90% of the allelic forms originated in the most recent 983 generations. For $N = 1\,000\,000$ (with the expected time since a common ancestor of $2\,000\,000$ generations), $1/2$ of the individuals in the pedigree lived, hence $1/2$ of the allelic forms originated, in the most recent 1861 generations; 90% of the individuals lived, hence 90% of the allelic forms originated in the most recent $495\,237$ generations.

We are not addressing questions such as the age of a mutant dependent on its frequency, which have been considered elsewhere (Watterson and Guess, 1977), merely the distribution of ages of mutants.

In addition to the overall shape of the ancestral pedigree, the branching structure within the ancestral pedigree is also quite similar for the branching process and Wright-Fisher models. Since essentially all of the branchings in the early ancestral pedigree are bifurcations, it suffices to show that the branching structure in recent generations is similar. This is true

because a branching process with Poisson progeny distribution conditioned on the final population size has a binomial progeny distribution. We state this formally as Result III.

Result III: The ancestral pedigree for a Wright-Fisher model is approximately the ancestral pedigree of an unconstrained branching process with Poisson progeny distribution.

Proof of Result III: One way to generate a Poisson distribution is as the number of events which occur in a Poisson process in a specified period of time. From this perspective, the Wright-Fisher model with constant population size can be obtained from the branching process with Poisson progeny distribution by increasing or decreasing the time that the Poisson process runs so that the total resultant number of progeny is N (i.e., the total for all individuals, hence all branching processes since each individual has an independent branching process). This entails adding branches to or removing branches from the branching process. The resultant progeny distribution is the Wright-Fisher model, since it is the Poisson distribution conditioned on final population size. Thus the Wright-Fisher model is obtained by adding branches to or removing branches from the unconstrained branching process each generation.

If a population has size N, then the standard deviation of the population size resulting from a Poisson progeny distribution with parameter $\lambda = 1$ is $\sqrt{N}$, hence on average approximately $.8\sqrt{N}$ of the branches will have to be added or removed from a branching process to obtain the Wright-Fisher model each generation ($.8$ is the average of $|z|$ with the standard normal distribution). Indeed N will change over time for a branching process, but cumulating these added and deleted branches across generations accounts for this. Half

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the generations should entail adding lineages, and half removing lineages. For example, for $N = 1,000,000$, going back 25 generations, $(1 - .8/1000)^{12.5} = .99$ and approximately 99% of the branches in an unconstrained branching process will be in the Wright-Fisher model. Similarly, approximately 1% of the branches in the Wright-Fisher pedigree will not be from the unconstrained branching process. Exchangeability of branches (an extra branch one generation may persist when an original branch is eliminated the next generation) will reduce the difference between the unconstrained branching process and Wright-Fisher pedigree. The ancestral pedigree 25 generations ago is less than 8% of the present population size. Going back 200 generations over 92% of the branches will be the same; the ancestral pedigree 200 generations ago is less than 1% of the present population size.

The Logistic Model

The fluctuation in population size in the above branching process model will be reduced if the Poisson distribution governing the number of progeny has parameter N_{eq}/N instead of 1, where N_{eq} is the equilibrium population size and N is $N(t)$, the population size at the time of reproduction. Since there will be N branching processes, each with expected value N_{eq}/N, the expected population size will be N_{eq} each generation. Furthermore, since each individual reproduces independently, the variance of the population size will be N_{eq} each generation (hence the standard deviation $\sqrt{N_{eq}}$).

The previous analyses cannot be applied to this model, because the growth (size) of different branches are not independent. However, the probability of fixation must still be the reciprocal of the initial frequency by symmetry. The expected time until fixation can be

shown to be $2N_{eq}$ generations by the diffusion approximation as indicated below.

Within each generation, the reproduction of the genes are independent Poisson branching processes, hence the reproduction of each type of allele is a Poisson branching process (Feller 1957). Furthermore, if one is considering only two different alleles, the number of alleles of each type, conditioned on the resultant population size, will have a binomial distribution (if each allele obeys a Poisson distribution, Feller 1957). Therefore the sampling variance will be $V_{\delta p} = \frac{p(1-p)}{N}$. Indeed, N is a random variable, but in the neutral case $V_{\delta p}$ occurs in the denominator of the integrand of the integral for fixation time (Kimura and Ohta 1969, Crow and Kimura 1970), hence the N is really in the numerator. Because the expected value of an integral is the integral of the expected value, N_{eq} can be used to calculate the expected fixation time. Thus this model gives the same fixation time as the Wright-Fisher model. The fixation probability is determined by the original population size $N(0)$, but the fixation time is determined by the expected population size (N_{eq}).

For the logistic branching process, the probability of extinction is equal to one, as it is for the regular branching process. This can easily be seen because it returns to size N_{eq} (in expectation) each generation, and there is a positive probability of having no progeny. In fact, the probability of extinction in any generation is $e^{-N_{eq}}$, which follows since the Poisson parameter is $\lambda = N_{eq}/N$, hence the probability of extinction for the entire population is $(e^{-\lambda})^N$. Note that this has the same expected time to fixation as the Wright-Fisher model by the diffusion argument.

However, for the regular branching process, although the probability of extinction is

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1, the expected time until extinction is infinite. (This follows easily from the probability of extinction $1 - 1/(2t)$, and can be shown rigorously using the error bound ϵ/t in Holte (1974).) With the logistic branching process, the probability of extinction being equal to $e^{-N_{eq}}$ provides that the expected time until extinction is $1/e^{-N_{eq}}$, by a geometric series.

Result IV: The ancestral pedigree for a logistic branching process is approximately the ancestral pedigree of an unconstrained branching process.

This is demonstrated by showing that the recent generations of the pedigree, which entail a significant reduction in pedigree size, are similar, and that the early generations also have a similar pedigree. The latter is true because the pedigree preceding recent growth is small and the time since the most recent common ancestor is the same for both branching processes, hence the early growth of the pedigree cannot be very different. The former requires analyzing how the Poisson distribution generates the branching process.

Proof of Result IV: Taking the derivative of the probability mass function for the Poisson distribution with respect to the parameter λ shows that increasing λ increases the number of all multiple sibships while decreasing the number of empty sibships, and decreasing λ decreases the number of multiple sibships and increases the number of empty sibships. The number of individuals with a single progeny has a higher order (i.e., smaller magnitude) decrease when λ is either increased or decreased. This provides a basis for viewing the branching process of a generation with λ not equal to one as a branching process for $\lambda = 1$ to which branches have been added (or from which branches have been removed). The random variable λ equals N_{eq}/N where N is a random variable with mean N_{eq} and standard

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deviation $\sqrt{N_{eq}}$, which means that on average approximately $.8\sqrt{N_{eq}}/N_{eq}$ of the branches will have to be added or removed from a $\lambda = 1$ pedigree (.8 is the average of $|z|$ with the standard normal distribution). Since lineages persist, these changes cumulate with the passage of generations. But half the generations should entail adding lineages, and half removing lineages. As in the comparison of the unconstrained branching process with the Wright-Fisher model, if $N = 1,000,000$, going back 25 generations, $(1 - .8/1000)^{12.5} = .99$ and approximately 99% of the branches in an unconstrained branching process will be in the logistic branching process. Similarly, approximately 1% of the branches in the logistic pedigree will not be from the unconstrained branching process. Exchangeability of branches (an extra branch one generation may persist when an original branch is eliminated the next generation) will reduce the difference between the unconstrained and logistic pedigree. The ancestral pedigree 25 generations ago is less than 8% of the present population size. Going back 200 generations over 92% of the branches will be the same; the ancestral pedigree 200 generations ago is less than 1% of the present population size.

The Case of Weak Selection

The classic result for the Wright-Fisher model is that the probability of fixation of an allele with relative fitness $1 + s$ is approximately $2s$ (Haldane 1927). Since this is based on the probability of extinction of a branching process independent of the rest of the population, it is more appropriate for the unconstrained branching process above (only the mutant and its descendants have the selective advantage) than for the Wright-Fisher model and it will be valid for the unconstrained branching process.

Fluctuation in the parameter of the Poisson process for the entire population will entail fluctuation in the value of $1+s$ if $1+s$ is defined as a relative viability. However, Ewens (1967) has found that for a fluctuating population size where $1+s$ represents a relative viability, the probability of fixation is $2s\tilde{N}/N(0)$, where $N(0)$ is the initial population size and $\tilde{N}$ is the harmonic mean of the population sizes over time. Hence if one is interested in the average probability of fixation for a mutant allele, this ratio should be weighted by the initial population size to calculate the probability of fixation of a new mutant, since the probability of a mutation occurring with a given initial population size should be proportional to that population size; this weighted average results in $2s\tilde{N}/\bar{N}$, where the arithmetic mean appears in the denominator. Hence there will be a slight reduction in the probability of fixation as contrasted to the Wright-Fisher model since the harmonic mean is less than the arithmetic mean. However, if immigration is the source of new "mutations", an unweighted mean should be taken which results in $(2s\tilde{N})/\tilde{N}$, i.e., the same result as for the Wright-Fisher model.

These results for probability of fixation of a selected allele assume that s is small, but not so small that selection is near-neutral ($s \ll 1$, but $4Ns > 1$).

Wright-Fisher model (constant population size, constan relative viability).

Discussion

This investigation was motivated by the question: is the branching process a reasonable approximation to the Wright-Fisher model only when an allele is rare? To that end, a logistic branching process which would limit population size fluctuation was introduced in

addition to the standard branching process. Analysis showed that the probability of fixation of a neutral allele and time until fixation of a neutral allele are the same for all three models. Furthermore, the entire coalescent (ancestral pedigree) is quite similar for all three models. This suggests that it may be appropriate to study branching processes to understand the dynamics of the changes in allele frequencies at all allele frequencies.

The use of branching process approximations to the Wright-Fisher model has been restricted to when alleles are rare because the constraint of constant population size entails that the branches cannot reproduce independently. But the constraint of constant population size is not realistic, population sizes do fluctuate in nature. The logistic branching process introduced in this manuscript may be more realistic than the Wright-Fisher model, even if the unconstrained branching process allows too much fluctuation in population size.

We did not quantify the magnitude of fluctuation of population size for the unconstrained branching process, but since the standard deviation of the change is $\sqrt{N}$ each generation, the cumulative affect would be quite large as N varies from generation to generation. The logistic branching process is modelled with parameter $\lambda = N_{eq}/N$ for the Poisson progeny distribution, hence the size of a population with $N_{eq} = 1000$ would be between 937 and 1063 ninety-five per cent of the time, which may be less variation than occurs in nature. But taken together, these models span much of the range of population variation which occurs.

The remarkable finding is that these branching process models are consistent with the Wright-Fisher model for probability of fixation of a neutral mutation, expected time until fixation of a neutral mutation, and probability of fixation of an advantageous mutation. The

probability of fixation of a neutral mutation is not surprising since it follows by symmetry. But there is not such a trivial argument to explain the latter two results. The entire structure (shape) of the ancestral pedigree is quite similar for these three models. In particular, this confirms that most mutations will be of relatively recent origin. This study buttresses the results for the Wright- Fisher model by showing that they hold for two other models. It also suggests that branching process models can be used more generally in population genetics.

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