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Dynamics of Finite Populations

II. A Time-Homogeneous Stochastic Process Describing the Ultimate Probability of and the Expected Time to Fixation or Loss of an Allele or Type in a Population of Variable Size[1]

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Summary. A time-homogeneous stochastic process was used to derive exact expressions for the ultimate probability of fixation or loss and the expected time to fixation or loss of an allele in a haploid population whose size is a Poisson random variable. The treatment included selection and multiple alleles.

1. Introduction

Genetic theories of finite populations have been developed dealing with the rate and probability of fixation of an allele and with its time to fixation (Kimura 1957, 1970, Felsenstein 1971, Watterson 1959, Carr and Nassar 1970). The limiting assumption in these studies is that of a constant population size. Ecological evidence shows that some populations vary in size over time (Andrewartha and Birch, 1954), hence in the study of the dynamics of gene frequencies in finite populations it is desirable to formulate models with variable population size. Karlin (1968) studied the rate of approach to homozygosity for a selectively neutral gene in finite stochastic models of variable population size. Cook and Nassar (1972), using independent branching processes, studied the time to fixation and the probability of survival of a selectively neutral gene in a finite population with a Poisson progeny distribution. There have been previous studies of the survival of a gene using independent branching processes having a Poisson progeny distribution. However, all of these studies were limited to populations of infinite size (Fisher 1930, Pollak 1966, Ohta and Kojima 1968, and others).

In this study we investigate in a finite haploid population of variable size with a Poisson progeny distribution the time to fixation and the probability of survival of a gene under selection.

2. The Model

Consider a population of n_0 haploid individuals of which k_0 are of type A_1 and $n_0 - k_0$ of type A_2. Assume that individuals reproduce independently of one another and generations discrete and that each individual has a progeny distribution that is Poisson with parameter α in type A_1 and β in type A_2. With that, the

$$Pr\text{ (an individual of type } A_1 \text{ has } n \text{ offspring)} = \frac{e^{-\alpha}\,\alpha^n}{n!}, \quad n = 0, 1, 2, \ldots, \tag{2.1}$$

$$Pr\text{ (an individual of type } A_2 \text{ has } n \text{ offspring)} = \frac{e^{-\beta}\,\beta^n}{n!}, \quad n = 0, 1, 2, \ldots \tag{2.2}$$

for some $\alpha > 0$, $\beta > 0$. The distribution of the population size of type A_1 in the next generation is the distribution of the sum of k_0 independent random variables each having the Poisson density (2.1). Also the distribution of the population size of type A_2 is the distribution of the sum of $(n_0 - k_0)$ independent random variables each having the Poisson density (2.2). The joint distribution of the population size of types A_1 and A_2 in the next generation is then the product of the A_1 and A_2 distributions.

The probability in the next generation of having k_1 individuals of type A_1 and $(n_1 - k_1)$ individuals of type A_2 given k_0 and $n_0 - k_0$ in the present generation is

$$Pr\,(K_1 = k_1, N_1 = n_1 | K_0 = k_0, N_0 = n_0) = \frac{e^{-k_0\alpha}(k_0\,\alpha)^{k_1}}{k_1!}\,\frac{e^{-(n_0-k_0)\beta}\,((n_0 - k_0)\,\beta)^{n_1-k_1}}{(n_1 - k_1)!}\,. \tag{2.3}$$

The stochastic process as described has a set of absorbing states (A)

$$A = \{(X, N) | X = 0 \text{ or } N,\ N = 0, 1, 2, \ldots\}$$

and a set of transient states (T)

$$T = \{(X, N) | 0 < X < N,\ X \text{ and } N \text{ integers}\}\,.$$

Assuming that the above process is time-homogeneous, the one step transition probability is represent-

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ed as

$$P((k, m), (i, j)) = e^{-k\alpha-(m-k)\beta}\frac{(k\,\alpha)^i}{i!}\,\frac{((m-k)\,\beta)^{j-i}}{(j-i)!}\,,$$
$$0 < k < m,\ 0 \leq i \leq j\,. \qquad (2.4)$$

When $\alpha \neq \beta$ there is selection acting in terms of differential reproduction of the two types.

3. Probability of Being in a Transient State

Let

$$\left.\begin{aligned} X^1(k, m) &= \sum_{(i,j)\,\varepsilon\, T} P((k, m), (i, j)); \quad (k, m)\ \varepsilon\ T \\ X^2(k, m) &= \sum_{(i,j)\,\varepsilon\, T} P((k, m), (i, j))\, X^1(i, j) \end{aligned}\right\} \quad (3.1)$$

and

$$X^n(k, m) = \sum_{(i,j)\,\varepsilon\, T} P((k, m), (i, j))\, X^{n-1}(i, j);$$
$$n \geq 2 \text{ and } (k, m)\ \varepsilon\ T$$

$X^n(k, m)$ is the probability that, starting from the transient state (k, m), the process remains in T for the next n transitions. Substituting (2.4) into (3.1) and using induction, we can show that

$$X^n(k, m) = 1 - e^{-k\alpha_n} + e^{-k\alpha_n-(m-k)\beta_n} - e^{-(m-k)\beta_n};$$
$$n = 1, 2, \ldots \qquad (3.2)$$

where

$$\left.\begin{aligned} \alpha_1 &= \alpha > 0 & \text{and}\quad \beta_1 &= \beta > 0 \\ \alpha_2 &= \alpha\,(1 - e^{-\alpha_1}) & \beta_2 &= \beta\,(1 - e^{-\beta_1}) \\ &\ \vdots & &\ \vdots \\ \alpha_n &= \alpha\,(1 - e^{-\alpha_{n-1}}) & \beta_n &= \beta\,(1 - e^{-\beta_{n-1}})\,. \end{aligned}\right\} \quad (3.3)$$

The sequences $\{\alpha_n\}$ and $\{\beta_n\}$ are decreasing sequences which have a limit of zero if $0 < \alpha \leq 1$ and $0 < \beta \leq$ ≤ 1. The limits are finite ($L_\alpha > 0$, $L_\beta > 0$) if $\alpha > 1$, $\beta > 1$. In the latter case L_α and L_β are the positive roots of $L_\alpha = \alpha\,(1 - e^{-L_\alpha})$ and $L_\beta = \beta\,(1 - e^{-L_\beta})$ respectively as shown by Cook and Nassar, 1972. Considering the limits of $\{\alpha_n\}$ and $\{\beta_n\}$ it is easy to see that

$$\lim_{n\to\infty} X^n(k, m) = 0 \text{ for } \alpha \text{ and/or } \beta \leq 1$$
$$= L \text{ for } \alpha \text{ and } \beta > 1\,.$$

In words, if the average number of progeny per individual of either or both types is equal to or less than 1, then with probability 1 a type will be eventually fixed or lost from the population. If the average progeny number of an individual in both types is larger than 1, there is a positive probability that both types remain indefinitely in the population. The above remarks can also be deduced from standard branching process theory.

4. Ultimate Probability of Fixation or Loss

In this section we inquire into the ultimate probability that a type is fixed or lost from a population. Let

$$\left.\begin{aligned} D^1(k, m) &= \sum_{j=1}^{\infty} P((k, m), (i, j)) \\ D^2(k, m) &= \sum_{j=2}^{\infty}\sum_{i=1}^{j-1} P((k, m), (i, j))\, D^1(i, j) \\ &\ \vdots \\ D^n(k, m) &= \sum_{j=2}^{\infty}\sum_{i=1}^{j-1} P((k, m), (i, j))\, D^{n-1}(i, j) \end{aligned}\right\} \quad (4.1)$$

where $D^n(k, jm)$ is the probability that the process is absorbed into the class $D = \{(n, n) | n = 1, 2, \ldots\}$ in the nth transition given the initial transient state (k, m).

Substituting (2.4) into (4.1) and using the induction argument, we can show that

$$D^n(k, m) = e^{-(m-k)\beta_n} - e^{-k\alpha_n-(m-k)\beta_n} +$$
$$+ e^{-k\alpha_n-(m-k)\beta_{n-1}} - e^{-(m-k)\beta_{n-1}}\,;\ n > 1\,. \qquad (4.2)$$

The ultimate probability of fixation is

$$D(k, m) = \sum_{n=1}^{\infty} D^n(k, m) = 1 - e^{-k\alpha-(m-k)\beta} +$$
$$+ \sum_{n=2}^{\infty} (e^{-k\alpha_n-(m-k)\beta_{n-1}} - e^{-k\alpha_n-(m-k)\beta_n}) \qquad (4.3)$$

if $0 < \beta \leq 1$ or

$$D(k, m) = e^{-(m-k)L_\beta} - e^{-k\alpha-(m-k)\beta} +$$
$$+ \sum_{n=2}^{\infty} (e^{-k\alpha_n-(m-k)\beta_{n-1}} - e^{-k\alpha_n-(m-k)\beta_n}) \qquad (4.4)$$

if $\beta > 1$.

The ultimate probability that type A_1 is lost from the population is

$$1 - D(k, m) = G(k, m)$$

where

$$G = \{(0, n) | n = 0, 1, 2, \ldots\}\,.$$

This includes the situation where loss is also due to population extinction.

It can be shown that

$$G(k, m) = 1 + \sum_{n=2}^{\infty} e^{-k\alpha_{n-1}-(m-k)\beta_{n-1}} - e^{-k\alpha_n-(m-k)\beta_{n-1}} \qquad (4.5)$$

if $0 < \alpha \leq 1$ or

$$G(k, m) = e^{-kL_\alpha} + \sum_{n=2}^{\infty} e^{-k\alpha_{n-1}-(m-k)\beta_{n-1}} -$$
$$- e^{-k\alpha_n-(m-k)\beta_{n-1}} \qquad (4.6)$$

if $\alpha > 1$.

The probability of ultimate loss, excluding the case of population extinction, can be derived as follows:

Let

$$C^1(k, m) = \sum_{j=1}^{\infty} P((k, m), (0, j)) \qquad (4.7)$$

and

$$C^n(k, m) = \sum_{j=2}^{\infty} \sum_{i=1}^{j-1} P((k, m), (i, j))\, C^{n-1}(i, j)$$

again substituting (2.4) into (4.7) we can show by induction that

$$C^n(k, m) = e^{-k\alpha_n} - e^{-k\alpha_{n-1}} - e^{-k\alpha_n-(m-k)\beta_n} + \\ + e^{-k\alpha_{n-1}-(m-k)\beta_n}$$

the ultimate probability of loss, excluding extinction, is

$$C(k, m) = \sum_{n=1}^{\infty} C^n(k, m) = 1 - e^{-k\alpha-(m-k)\beta} + \\ + \sum_{n=2}^{\infty} e^{-k\alpha_{n-1}-(m-k)\beta_n} - e^{-k\alpha_n-(m-k)\beta_n} \quad (4.8)$$

if $0 < \alpha \leq 1$. If $\alpha > 1$, e^{-kL_α} replaces 1 in (4.8).

5. Expected Time to Fixation or Loss

Let $E(k, m)$ denote the expected time to absorption given that the process began in the transient state (k, m). Then

$$E(k, m) = \sum_{n=1}^{\infty} n(G^n(k, m) + D^n(k, m)) \quad (5.1)$$

following the same argument we presented previously (Cook and Nassar, 1972) we can show that

$$E(k, m) = 1 + \sum_{n=2}^{\infty} 1 + e^{-k\alpha_n-(m-k)\beta_n} - e^{-k\alpha_n} - \\ - e^{-(m-k)\beta_n} . \quad (5.2)$$

The series in (5.2) diverges only when $\alpha > 1$ and $\beta > 1$; otherwise it converges. $E(k, m)$ is not defined for $[\alpha > 1, \beta > 1]$, the case where the probability of ultimate absorption is less than 1. $E(k, m)$ is finite where the probability of ultimate absorption of the stochastic process is 1. We can also define $E'(k, m)$ as the expected time to fixation or loss of an allele given that the population does not go to extinction.

$$E'(k, m) = \sum_{n=1}^{\infty} n(C^n(k, m) + D^n(k, m)/(C(k, m) + \\ + D(k, m))) . \quad (5.3)$$

The expected time to loss of type A_1, given that loss occurs, is:

$$E_L(k, m) = \sum_{n=1}^{\infty} n(G^n(k, m))/G(k, m) \quad (5.4)$$

or

$$E'_L(k, m) = \sum_{n=1}^{\infty} n(C^n(k, m))/C(k, m) \quad (5.5)$$

similarly, for fixation

$$E_f = \sum_{n=1}^{\infty} n(D^n(k,m))/D(k, m) \quad (5.6)$$

6. r Types

The results of the previous sections can be extended to include a population with r types of individuals. The one step transition probability is then

$$P((i_1, i_2, \ldots, i_{r-1}, m), (j_1, j_2, \ldots, j_{r-1}, q)) = \\ = \exp\left(-\sum_{k=1}^{r} i_k \alpha_k\right) \prod_{k=1}^{r} \frac{(i_k\, \alpha_k)^{j_k}}{j_k!} \quad (6.1)$$

where

$$i_r = m - \sum_{k=1}^{r-1} i_k; \quad j_r = q - \sum_{k=1}^{r-1} j_k$$

and

$\alpha_k =$ the average progeny number per individual of type k.

Ultimate Probability of Absorption

Let $X^n(i_1, i_2, \ldots, i_{r-1}, m) =$ probability that starting from the transient state $(i_1, i_2, \ldots, i_{r-1}, m)$ at least two types will still be present in the population in the next n generations. The process is defined to be transient if at least two types are present in the population. Analogous to the previous presentation of Section 3, we can show that

$$X^n(i_1, i_2, \ldots, i_{r-1}, m) = 1 - \sum_{v=1}^{r} \exp\left(-\sum_{\substack{k=1 \\ k \neq v}}^{r} i_k \alpha_{k,n}\right) + \\ + (r-1) \exp\left(-\sum_{k=1}^{r} i_k \alpha_{k,n}\right), \quad (6.2)$$

where

$$\left.\begin{aligned} \alpha_{k,1} &= \alpha_k \\ \alpha_{k,2} &= \alpha_k\,(1 - e^{-\alpha_{k,1}}) \\ &\vdots \\ \alpha_{k,n} &= \alpha_k\,(1 - e^{-\alpha_{k,n-1}}) . \end{aligned}\right\} \quad (6.3)$$

As expected, at least $r - 1$ of the $\{\alpha_k\}$ sequences must be equal to zero in the limit if absorption is to occur with probability 1. This implies that $r - 1$ of the types must have an average progeny number per individual (α_k) equal to or less than one.

Ultimate Probability of Fixation

Let $D_n^k(i_1, i_2, \ldots, i_{r-1}, m) =$ the probability that the kth type $(k = 1, 2, \ldots, r)$ is fixed in the population at the nth generation or transition, given the initial transient state $(i_1, i_2, \ldots, i_{r-1}, m)$.

$$D_k(i_1, i_2, \ldots, i_{r-1}, m) = \sum_{n=1}^{\infty} D_k^n(i_1, i_2, \ldots, i_{r-1}, m) =$$

= the ultimate probability of fixation of type k.

Analogous to section 4 we can show that

$$D_k^n(i_1, i_2, \ldots, i_{r-1}, m) = \exp\left[-\sum_{\substack{j=1\\ j\neq k}}^{r} i_j\alpha_{j,n}\right] - \exp\left[-\sum_{j=1}^{r} i_j\alpha_{j,n}\right] - \exp\left[-\sum_{\substack{j=1\\ j\neq k}}^{r} i_j\alpha_{j,n-1}\right] + \exp\left[-i_k\alpha_{k,n}\right]\exp\left[-\sum_{\substack{j=1\\ j\neq k}}^{r} i_j\alpha_{j,n-1}\right]. \quad (6.4)$$

Under the present theory it is possible to define and compute several forms of loss of a gene. A gene, for example, can be lost when all others are still segregating. It is only when the population is ultimately monomorphic with probability one that the ultimate probability of loss can be computed as one minus the ultimate probability of fixation, (6.4). No other definitions of loss will be considered here.

Other expressions analogous to those of Sections 4 and 5 for r types in the population can be written in terms of (6.2) and (6.4). For example, the expected time until the population becomes monomorphic can be written as

$$1 + \sum_{n=2}^{\infty} X^n(i_1, i_2, \ldots, i_{n-1}, m)\,.$$

Other analogies are also straightforward.

7. Discussion

Fisher (1930) was the first to study the probability of survival of an individual gene in a population of infinite size. Assuming a Poisson progeny distribution he calculated the probability of survival at generation n and in the limit for a gene that is neutral and with a 1% selective advantage. In our formulation the probability of survival at generation n is

$$X^n(k, m) + \sum_{j=1}^{n} D^j(k, m)\,, \quad (7.1)$$

where the first term represents the probability at time n that the gene is still segregating in the population and the second term the probability that it is fixed. Our approach reduces to that of Fisher when the population size is infinite. This is shown as follows: Taking the limit of (7.1) as $m \to \infty$ one gets

$$\lim_{m\to\infty}\left[X^n(k, m) + \sum_{j=1}^{n} D^j(k, m)\right] = 1 - e^{-k\alpha_n}\,.$$

For a single mutant

$$X^n(1, \infty) = 1 - e^{-\alpha_n} = 1 - e^{-\alpha(1-e^{-\alpha_{n-1}})} = = 1 - e^{-\alpha X^{n-1}(1,\infty)} \quad (7.2)$$

which is essentially Fisher's recursive relationship for the probability of survival to generation n. The ultimate probability of survival, $X^{\infty}(1, \infty)$, is

$$\left.\begin{aligned} \lim_n X^n(1, \infty) &= \lim_n \left(1 - e^{-\alpha X^{n-1}(1,\infty)}\right) \\ X^{\infty}(1, \infty) &= 1 - e^{-\alpha X^{\infty}(1,\infty)}\,. \end{aligned}\right\} \quad (7.3)$$

An approximate solution to equation (7.3) when $\alpha - 1$ is small and positive can be deduced from Bartlett (1966, page 43) as

$$\begin{aligned} X^{\infty}(1, \infty) &= 1 - e^{-2(\alpha-1)/\sigma^2} \\ &\doteq 2(\alpha - 1)/\alpha \quad \text{for a Poisson} \end{aligned} \quad (7.4)$$

which is equal to 0.0197 when $\alpha = 1.01$ (Table 1). The ultimate probability of survival of a single gene in a finite population is seen to be larger than that of a large population. The increase is due to an increase in the probability of fixation of the gene as a result of random genetic drift due to small population size.

Kimura and Ohta (1969) calculated that the time to fixation (excluding loss) of a neutral mutant gene in a diploid random mating population of constant size N_e is approximately equal to $4\,N_e$. They also reported on the time to loss (excluding fixation) for several population sizes. Although our results are strictly applicable to a haploid model, it is interesting to note that the time to fixation or loss (from equations 5.5 and 5.6) of a neutral mutant gene in a haploid population of stable size ($\alpha = \beta = 1$) is approximately the same as that in a random mating diploid population whose number of gametes ($2\,N_e$) is equal to the mean (m) of the haploid population (Table 2). In all cases, however, results of the haploid case were slightly less than the corresponding results of the diploid case. The correspondence of the haploid and diploid results ceases when the haploid population is no longer stable in size. If gene substitution occurs when the population is decreasing in size ($\alpha = \beta = 0.95$), then there is a decrease in the time to fixation or loss of the gene as compared to that of the stable size. An increase in the time to fixation is observed, however, if the population is increasing in size during gene substitution ($\alpha = 1.01$, $\beta = 1.0$).

Table 1. *The probability of survival of a mutant gene with a one percent selective advantage ($\alpha = 1.01, \beta = 1$) in a population of initial size 100 and infinity*

Generation	Probability gene is segregating $m = 100$	Probability gene is fixed $m = 100$	Probability of survival $m = \infty$
1	0.63578	0.0	0.6358
3	0.38033	0.0	0.3803
7	0.21749	0.0	0.2175
15	0.12169	0.92×10^{-6}	0.1217
31	0.06854	0.19×10^{-3}	0.0687
63	0.03889	0.24×10^{-2}	0.0409
127	0.02125	0.007807	0.0271
limit	0.0	0.02414	0.0197

Table 2. *The expected time to fixation and to loss and the ultimate probability of fixation of a mutant gene*

Parameter		Population size		Time to loss		Time to fixation	Ultimate prob. of fixation
β	α	haploid m	diploid 2 N	haploid	diploid (Kimura '69)		
1	1	20	20	5.69	6.3	37.97	0.0488
1	1	60	60	7.69	8.2	117.01	
1	1	100	100	8.61	9.3	192.04	
0.95	0.95	60		4.42		31.01	
0.95	0.95	20		3.78		16.66	0.0476
0.95	0.96	20		3.84		17.42	0.0532
0.95	1.0	20		3.97		21.23	0.0832
0.8	0.81	20		2.45		7.93	0.0472
0.8	0.85	20		2.54		8.36	0.0625
1	1.01	20		5.36		94.68	0.06

Table 3. *Comparison of theoretical (Poisson case) and Monte Carlo (negative binomial case) results for the time to fixation and to loss and for the probability of fixation of a neutral mutant gene in a population of initial size 10*

Progeny distribution	Time to fixation	Time to loss	Probability of fixation
$\alpha = \beta = 1$			
Poisson	18.19	4.54	0.1
negative binomial	16.78 ± 4.4	4.34 ± 0.56	0.101 ± 0.022
$\alpha = 1.02,\ \beta = 1$			
Poisson	47.22	4.20	0.116
negative binomial	32.57 ± 8.59	4.18 ± 0.44	0.104 ± 0.015

When the size of the population is constant, it is known that the time to fixation of a mutant gene decreases with an increase in its selective advantage. If the population is growing in size, however, the time to fixation is seen to increase with an increase in its selective advantage. This is also true when the population is growing in size for the first few generations and then stabilizes (unpublished work). The results of Table 2 show also that a mutant gene with a selective advantage has a higher ultimate probability of fixation when the population is growing in size than when it is decreasing in size (compare for instance $m = 20$, $\alpha = 1.01$, $\beta = 1.0$ with $m = 20$, $\alpha = 0.96$, $\beta = 0.95$).

The results of our model rest on the assumption of a Poisson progeny distribution per individual. Very little empirical evidence is known to support or refute this assumption. One other distribution that is sometimes assumed for an offspring distribution is the negative binomial. In a human population from the U.S. Census data, 1950, Kojima and Kelleher (1962) found a good fit of a negative binomial to the distribution of offspring per family. The variance of the distribution was found to be twice its mean.

On the basis that a negative binomial might present at times an alternative to the Poisson distribution we thought that it would be of interest to examine the effects on our results when a negative binomial progeny distribution per individual is assumed. From (7.4) the ultimate probability of survival of a mutant gene in a population of infinite size when the offspring distribution is a negative binomial

$$\left(P(X = j) = \binom{-r}{j} p^r (-q)^j, \quad j = 0, 1, \ldots\right)$$

with $\alpha = r\,q/p$ and $\sigma^2 = r\,q/p^2$ is

$$2\left(1 - \frac{1}{\alpha}\right)p \qquad (7.5)$$

where p $(0 < p < 1)$ is a parameter of the distribution. From (7.4) and (7.5) the ratio of the ultimate probability of fixation of a Poisson to that of a negative binomial is $1/p$. This ratio approaches 1 as $p \to 1$ and approaches ∞ as $p \to 0$. When the variance exceeds the mean the ultimate probability of fixation decreases from that of a Poisson. With a variance equal to twice the mean ($p = 1/2$ for example) the ultimate probability of fixation is expected to be 1/2 that of a Poisson. In finite populations, however, the difference between a Poisson and a negative binomial is not expected to be as great because of drift.

In order to study the effects a negative binomial progeny distribution might have on the ultimate probability of fixation and on the time to fixation in a finite population, a simulation study was done. The simulation techniques were as described by Cook and Nassar (1972). A negative binomial distribution was assumed with a variance equal to twice the mean ($p = 1/2$). Two cases were considered: 1. $\alpha = \beta = r\,q/p = 1$ and 2. $\alpha = r_1\,q/p = 1.02$, $\beta = r_2\,q/p = 1.0$. In both cases the initial population size was 10 with $k = 1$. Individuals were assumed to reproduce independently. The data of Table 3, based on 180 replications for case 1 and 300 replications for case 2 show that for a neutral mutant gene ($\alpha = \beta = 1$) there was no difference in results between a Poisson or a negative binomial progeny distribution. For a gene with a selective advantage, however, ($\alpha = 1.02$, $\beta = 1$) the time to fixation was noticeably reduced from that of a Poisson.

The assumption in our model of independence in reproduction among different individuals is not expected to be true for some populations. The assumption will particularly fail where a population has reached its limit of growth (set forth by limiting resources) and where competition among individuals is likely to be present. It is important to note, however, that when the initial population size is small, the substitution of a gene can be completed before the population reaches its limit of growth and hence when it is still likely that individuals reproduce independently of one another. The assumption that the population can grow infinitely large (a consequence of the Poisson distribution) is probably not true of many populations. However, a simulation study (Cook and Nassar 1972) of the same model where the transition probabilities were adjusted to exclude the status $N_t > 6\,m$ (N_t = population size at time t) did not significantly alter our conclusions. The assumption of a constant selective pressure from generation to generation might be restrictive when one considers that certain populations are known to fluctuate in epoch and from generation to generation. The relaxation of this assumption is dealt with in a future paper.

Literature

1. Andrewartha, H. G., Birch, L. C.: The Distribution and Abundance of Animals. Chicago: University of Chicago Press 1954. — 2. Bartlett, M. S.: An Introduction to Stochastic Processes with Special Reference to Methods and Applications. Cambridge: Cambridge University Press 1966. — 3. Carr, R. N., Nassar R. F.: I. Ultimate probability of fixation of a favorable allele. Biometrics **23**, 41—49 (1970). — 4. Carr, R. N., Nassar, R. F.: II. Expected time to fixation or loss of an allele. Biometrics **26**, 221—227 (1970). — 5. Cook, R. D., Nassar, R. F.: I. The expected time to fixation or loss and the probability of fixation of an allele in a haploid population of variable size. Biometrics **28**, 373—384 (1972). — 6. Felsenstein, J.: The rate of loss of multiple alleles in finite haploid populations. Theoretical Population Biology **2**, 391—403 (1971). — 7. Fisher, R. A.: The Genetical Theory of Natural Selection. Oxford: Oxford University Press 1930. — 8. Karlin, S.: Rates of approach to homozygosity for finite stochastic models with variable population size. Am. Naturalist **102**, 443—455 (1968). — 9. Kimura, M.: Some problems of stochastic processes in genetics. Ann. Math. Statisti. **28**, 882—901 (1957). — 10. Kimura, M., Ohta, T.: The average number of generations until extinction of an individual mutant gene in a finite population. Genetics **63**, 701—709 (1969). — 11. Kimura, M., Ohta, T.: Probability of fixation of a mutant gene in a finite population when selective advantage decreases with time. Genetics **65**, 525—534 (1970). — 12. Kojima, K., Kelleher, T. M.: Survival of Mutant Genes. The Am. Naturalist. **XCVI**, 329—345 (1962). — 13. Ohta, T., Kojima, K.: Survival probabilities of new inversions in large populations. Biometrics **24**, 501—516 (1968). — 14. Pollak, E.: Some effects of fluctuating offspring distribution on the survival of a gene. Biometrika **53**, 391—396 (1966). — 15. Watterson, G. A.: A new genetic population model and its approach to homozygosity. Ann. Human Genet. **23**, 204 to 220 (1959).

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