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# The time of detection of recessive visible genes with non-random mating

ARMANDO CABALLERO*, ALISON M. ETHERIDGE[1] AND WILLIAM G. HILL
*Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, Scotland*
[1] *Department of Mathematics and Statistics, University of Edinburgh, Mayfield Road, Edinburgh EH9 3JZ, Scotland*

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**Summary**

Expressions for the probability and average time of detection of a recessive visible gene in populations where there is partial selfing or partial full-sib mating are presented. A small increase in the proportion of inbred matings greatly reduces the average time until detection and increases the proportion detected. Unless the proportion of inbred matings or the population size is very small, the time and proportion detected are approximately independent of the population size.

## 1. Introduction

Robertson (1978) investigated the problem of ascertaining the average number of generations until detection of a recessive visible mutant initially present in single copy in a finite population. This is important in interpreting whether a recessive gene has appeared by mutation or was already present in the base population in artificial selection schemes. It has also relevance from an evolutionary viewpoint as the time to observation of, for example, spontaneous mutations, crossover events or mutant insertions.

Using transition matrix methods and simulation, he showed that for monoecious random mating populations of size $N$ with selfing permitted, the mean time to detection is close to $2N^{\frac{1}{3}}$ generations with a coefficient of variation of about $\frac{2}{3}$ and, if selfing is prohibited, this time increases by a little over one generation. Karlin & Tavaré (1981*a–c*) used a diffusion approximation, confirming the time-scale of $N^{\frac{1}{3}}$, and analysed a number of variants of the basic problem such as differential viability selection forces or partial penetrance of the heterozygote carriers. Santiago (1989) used simulation to study the effect of several systems of matings frequently used in laboratory experiments, such as random pair mating, within-family selection and circular mating, further confirming the generality of the scale $N^{\frac{1}{3}}$ found by Robertson.

In all these papers random mating of the reproductive individuals was assumed, except for the circular mating scheme investigated by Santiago (1989). In many plants, however, there is much self-fertilization (see, e.g. Schemske & Lande, 1985), which must affect the time of appearance of recessive homozygotes.

With random mating, a shortening of the time to detection can be obtained only by increasing the number of examined progeny. Karlin & Tavaré (1981*b*) suggested that non-random mating patterns be investigated for their influence on the early detection of recessive mutants. Caballero, Keightley & Hill (1991) found that a scheme where many full-sib matings are performed among the selected individuals would increase the fixation probability of recessive genes without reducing that for additive genes or delaying times to fixation. In such schemes with partial full-sib mating and random mating, the time until detection of recessives is expected to be reduced compared to that from a random mating population.

Branching process approximations for calculating the probability of detection of a recessive visible gene in successive generations for populations with partial selfing or partial full-sib mating and random mating are presented in this paper and checked and extended by transition matrix methods and stochastic simulation. It is found that a small proportion of inbred matings causes a large reduction in the time to detection and this time is nearly independent of the population size, unless the proportion of inbred matings or the population size is very small.

* Corresponding author.

## 2. Transition matrix and simulation analyses

For partial selfing, we assume a breeding population of size $N$ initially with one or more copies of a mutant gene ($A'$) in heterozygous condition, the remainder being the wild-type allele ($A$). Every generation, individuals are screened for recessive homozygotes $A'A'$ and, as soon as any appears, the process is stopped. The transition of the breeding population can be described by the number $i$ ($0 \leqslant i \leqslant N$) of heterozygous $AA'$ individuals, the remainder being homozygous wild-type $AA$, with an additional killing state ($i = N+1$) denoting detection of a homozygote mutant ($A'A'$), i.e. including all possible states of the population where there is at least one $A'A'$ individual. Assume that the fitnesses of $AA$ and $AA'$ are 1 and $1+s$, respectively. Then, for ($0 \leqslant i \leqslant N$) the frequency of $A'$ after selection ($q$) is $q = [i(1+s)/N]/[1+is/N]$ and the expected genotypic frequencies of offspring are

$$f_{AA} = x(1-3q/4)+(1-x)(1-q)^2,$$

$$f_{AA'} = xq/2+(1-x)\,2q(1-q),$$

$$f_{A'A'} = xq/4+(1-x)q^2,$$

where $x$ is the proportion of selfing. Each generation, all breeding individuals and perhaps others are screened for the recessive. It is also possible that the recessive homozygote has lower viability than the wild type or heterozygote. To incorporate both of these possibilities, let $K$ be an effective scoring rate, the ratio of the number of screened to reproductive individuals multiplied by the viability of the mutant homozygote. Thus, for example, $K = 1$ means $N$ individuals examined with 100% viability of the mutant homozygote or, alternatively, $2N$ individuals examined and viability 50%, etc.

The transition probability matrix with elements $m_{ij}$ denoting the conditional probability the population is in state $j$ at generation $t+1$ given it is in state $i$ at generation $t$, is defined by

$$m_{ij} = \binom{N}{j}(f_{AA})^{N-j}(f_{AA'})^{j}(1-f_{A'A'})^{N(K-1)},$$

$m_{i,N+1} = 1-(1-f_{A'A'})^{NK}$, $m_{N+1,j} = 0$, $m_{N+1,N+1} = 1$ $(i,j = 0,1,\ldots,N)$.

Note that loss of the mutant and its detection (states $i = 0$ or $N+1$) are absorbing states.

Denote by $\mathbf{d}$ the vector with elements $d_i = m_{i,N+1}$ and $\mathbf{Q}$ the matrix with elements $q_{ij} = m_{i,j}$ for $i,j = 1, 2, \ldots, N$, $\mathbf{I}$ the identity matrix and $\mathbf{v}$ the vector $v_1 = 1$, $v_i = 0$ ($i = 2, 3, \ldots, N$) for one initial mutant present. Then, using results from Kemeny & Snell (1960), the asymptotic probability of detection or total proportion of (conceptual) replicates where the mutant is detected ($P$) is

$$P = \mathbf{v}'(\mathbf{I}-\mathbf{Q})^{-1}\mathbf{d},$$

the average time to detection ($T$) is

$$T = \mathbf{v}'(\mathbf{I}-\mathbf{Q})^{-2}\mathbf{d}/P,$$

and the standard deviation of the time to detection ($SD$) is

$$SD = \{[\mathbf{v}'(\mathbf{I}+\mathbf{Q})(\mathbf{I}-\mathbf{Q})^{-3}\mathbf{d}/P]-T^2\}^{\frac{1}{2}}.$$

For a dioecious model with partial full-sib mating, simulation was carried out. One heterozygote for the mutant was initially present in a population of size $N$ (equal number of males and females) with, otherwise, wild-type homozygotes. Among the reproductive individuals full-sibs were mated whenever they were available, otherwise at random. Selection forces were simulated by truncation selection. The number of progeny from each pair was multinomially distributed and a total $KN$ was screened. The procedure was continued until loss or detection of the mutant as a homozygote and each simulation was replicated 10000 times. For details of the procedure see Caballero *et al.* (1991).

## 3. Branching process approximations

In a monoecious population of size $N$ with random union of gametes, the expected frequency of homozygotes in generation $t+1$ for a mutant present in single copy in generation $t$ is $1/4N^2$. Thus, the probability of detection as a homozygote if $N$ individuals are examined in generation $t+1$ is $1-[1-(1/4N^2)]^N \approx 1/4N$. If the proportion of selfing is $x$, the expected frequency of homozygotes is $x/4N$ and the probability of detection with $N$ offspring examined is approximately $x/4$. Therefore, the probability of detection will be a function of $x$ rather than $N$ if $x \gg 1/N$. An analogous argument can be made for a dioecious population with partial full-sib mating. The probability of detection in successive generations can, thus, be obtained for $x \gg 1/N$ by assuming a branching process in which mutant homozygotes can arise only from inbred matings.

### (i) *Partial selfing*

In a large population with partial selfing, it is assumed that homozygotes for the mutant arise only from self-fertilization of heterozygote carriers. Thus, the number of mutant homozygotes ($A'A'$) from a single heterozygote is Poisson distributed with index

$$\rho = x(1+s)/4,$$

where $x$ is the proportion of selfing and $s$ is defined as above. Hence, the probability that a heterozygote at generation $t$ is not detected by a homozygote offspring at generation $t+1$ is

$$\alpha = \exp[-K\rho],$$

where $K$ is defined as above.

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Heterozygotes ($AA'$) can arise from selfing, with probability $x(1+s)/2$, or from an outcross between a heterozygote and a wild type homozygote, with probability $(1-x)(1+s)$. Thus, their number can be assumed independently Poisson distributed with index

$$\mu = (1-x/2)(1+s).$$

Hence, the probability ($Pr[h]$) that a heterozygote has $h$ heterozygote offspring is given by $Pr[h] = e^{-\mu}\mu^h/h!$, with probability generating function

$$G[\zeta] = \sum_{h=0}^{\infty} Pr[h]\,\zeta^h = \exp[\mu(\zeta-1)].$$

The probability there are no mutants detected up to generation $t+1$ is given by the probability generating function of the total number of $AA'$ to generation $t$,

$$\Psi_{t+1}(\alpha) = \sum_{n=1}^{\infty} \alpha^n\, Pr[z_t = n],$$

where $z_t$ is the total number of heterozygotes to generation $t$. For simplicity, we will denote $\Psi_t(\alpha)$ as $\Psi_t$. Now, $\Psi_1 = \alpha$ as there is one heterozygote at generation 0, and from standard branching process theory

$$\Psi_{t+1} = \alpha G[\Psi_t] = \alpha \exp[\mu(\Psi_t - 1)]$$

(see Feller, 1968, p. 298). Substituting and rearranging,

$$\Psi_{t+1} = \exp\{(1+s)[(1-x/2)\,\Psi_t - (1-x/2+Kx/4)]\}, \quad (1)$$

with initial value $\Psi_0 = 1$. The probability of detection ($P_t$) up to and including generation $t$ is, therefore,

$$P_t = 1-\Psi_t.$$

The total proportion detected ($P$) is obtained by setting $\Psi_{t+1} = \Psi_t = \Psi$. For the simplest case of $K = 1$ and $s = 0$, a second order approximation, $P^2 + xP - x/2 = 0$, obtained from (1), is adequate. If there are initially $h$ heterozygotes, equation (1) is given by $(\Psi_{t+1})^h$ and the total proportion detected ($P_{(h)}$) can be directly obtained from the proportion detected with one initial homozygote ($P_{(1)}$) by $P_{(h)} = 1-(1-P_{(1)})^h$. Iteration of equation (1) also enables the average time to detection and its variance to be calculated.

(ii) *Partial full-sib mating*

In this case, assuming pair mating, the breeding population is completely described every generation by the number $S$ (single) of matings of the type $AA \times AA'$ and $D$ (double) of the type $AA' \times AA'$.

In a large population, the number of matings of type $j$ when there is one mating of type $i$ in the previous generation can be assumed Poisson distributed with index ($\mu_{ij}$)

$$\begin{aligned} \mu_{SS} &= (1-x/2)(1+s), \\ \mu_{SD} = \mu_{DD} &= (x/4)(1+s)^2, \\ \mu_{DS} &= (1-3x/4)(1+s), \end{aligned} \quad (2)$$

where $x$ is now the proportion of full-sib matings and $1+s$ is the relative viability of the mutant heterozygote.

The probability ($\alpha$) that a mutant homozygote is not detected from the offspring of a $D$ mating is

$$\alpha = \exp[-K/2], \quad (3)$$

where $K$ is defined as above.

The derivation of the recurrence equation to calculate the probability of no detection (shown in the Appendix) is similar to that for partial selfing except that there is now a two state branching process and two recurrence equations have to be considered for the types $S$ and $D$. Assuming initially one heterozygote (i.e. one $S$ mating), the probability that no recessive homozygotes will appear up to and including generation $t+1$ ($\Phi_{t+1}$) is

$$\begin{aligned} \Phi_{t+1} = \exp\{&(1-x/2)(1+s)(\Phi_t - 1) + (x/4)(1+s)^2 \\ &\times [\Phi_t \exp\{(x/4)(1+s)(1-\Phi_{t-1}) - (K/2)\} - 1]\}, \end{aligned} \quad (4)$$

with initial value $\Phi_1 = 1$. The probability of detection up to and including generation $t$ is $P_t = 1-\Phi_t$ or $1-(\Phi_t)^h$ for $h$ initial $S$ matings. Analogously to the selfing case, the total proportion detected for $K = 1$ and $s = 0$ can be well approximated by a second degree equation,

$$P^2 + Px(1-e^{-\frac{1}{2}}/2) - x(1-e^{-\frac{1}{2}})/2 \simeq 0.$$

Equation (4) can be iterated for successive generations to estimate the average time to detection and its variance.

## 4. Results

Figure 1 shows transition matrix results for partial selfing, neutrality ($s = 0$) and examination of only the breeding individuals ($K = 1$), plotted against the coefficient of inbreeding due to nonrandom mating, a function $F = x/(2-x)$ of the average number of selfing progeny, $x$ (see, e.g., Hedrick & Cockerham, 1986), and expectations calculated by means of equation (1). In addition, expected values for partial full-sib mating [eq (4)] are also shown for comparison. In this case, $F = x/(4-3x)$, for a given proportion $x$ of full-sib matings (Li, 1976, p. 245).

Whilst a reduction in the time to detection with inbreeding is expected, a striking feature from these figures is the large effect of a small increase in $F$ on reducing the time to detection and increasing the

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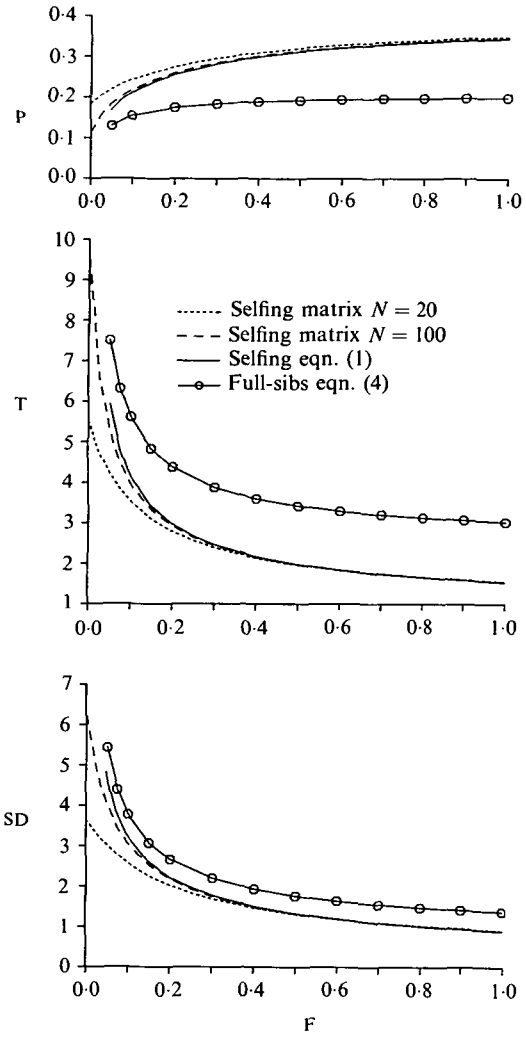


Fig. 1. Probability of detection as a homozygote ($P$) of a mutant initially present in single copy, average time (generations) until detection ($T$) and standard deviation of this time ($SD$), plotted for varying values of $F$. Transition matrix results for monoecious populations with $N = 20$ and $N = 100$. Expectations for monoecious [eqn (1)] and dioecious [eqn (4)] populations. $K = 1$, $s = 0$.

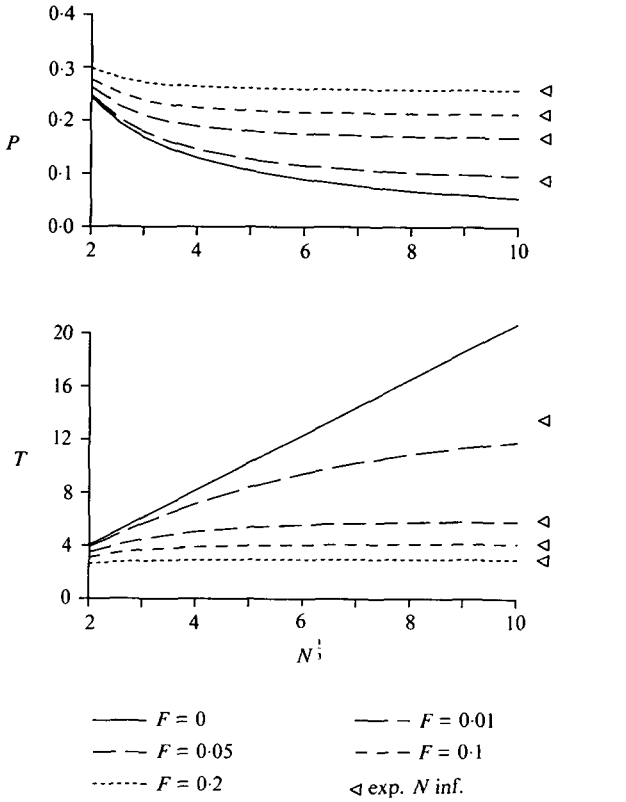


Fig. 2. Probability of detection as a homozygote ($P$) of a mutant initially present in single copy and average time (generations) until detection ($T$) for different values of $F$ and varying population size ($N$). Transition matrix results for monoecious populations with $K = 1$, $s = 0$. Expectations for infinite $N$ from eqn (1) indicated by arrows.

proportion detected. For $F = 0{\cdot}05$, for instance, which would be attained with only 9% selfing, the time to detection for $N = 100$ and random mating is reduced, and the proportion detected is increased, by about 40%. For all values of $F$, the standard deviation of the time to detection is approximately $\frac{2}{3}$ of its mean, as for random mating and other systems of mating (Robertson, 1978; Santiago, 1989).

Observed and expected values for partial selfing agreed well for values of $F > 0{\cdot}1$ (for $N = 20$) and $F > 0{\cdot}05$ (for $N = 100$) as predicted above. Independence of $N$ for large values of $F$ observed in Fig. 1 can be seen in more detail in Fig. 2, where the proportion detected and average time to detection for different population sizes are plotted for small values of $F$ [expectations for infinite $N$ from eq (1) are shown with arrows]. The implication is that, the greater the population size, the greater the reduction in time to detection for a fixed proportion of inbred matings, relative to that with random mating.

The average time to detection with partial full-sib mating is always about 1.5 generations more than with partial selfing for the same value of $F$ (Fig. 1). The proportion detected and the variance of the time to detection also behave similarly for both systems of partial inbreeding, though an increased proportion of full-sib matings has always a slightly smaller effect than an increased proportion of selfing. Stochastic simulation was used to check the theoretical expectations for partial full-sib mating, showing a very good agreement between observed and expected values. For example, for $N = 100$, $F = 0{\cdot}17$, $K = 2$ and $s = 0{\cdot}1$, values of $T$, $P$ and $SD$ were $4{\cdot}33 \pm 0{\cdot}03$, $0{\cdot}32 \pm 0{\cdot}00$ and $2{\cdot}52 \pm 0{\cdot}34$, respectively from simulation, and 4·05, 0·30 and 2·27, respectively from equation (4).

Transition matrix results for different values of $K$ (the ratio of examined to reproductive individuals times the viability of the mutant homozygote), coefficient of selection of the heterozygote ($s$) and initial number of heterozygote mutants ($h$) are shown in Table 1. The time to detection for random mating ($F = 0$) and $K = 1, s = 0$ agrees well with its prediction ($2N^{\frac{1}{3}}$ or, more exactly, $2{\cdot}09N^{\frac{1}{3}}$, Karlin & Tavaré, 1981 *a*).

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Table 1. *Transition matrix results (N = 100) for the proportion detected (P), the average time to detection (T) and its standard deviation (SD) for partial selfing and different degrees of inbreeding (F), ratio of number of examined to reproductive individuals times the viability of the recessive homozygote (K) (in all cases, at least N individuals are screened), selective advantage of the heterozygote (s) and initial number of heterozygotes carriers (h)*

| | $s = 0$ $h = 1$ | | | | $K = 1$ $h = 1$ | | | $s = 0$ $K = 1$ | |
|---|---|---|---|---|---|---|---|---|---|
| | $K = \frac{1}{2}$ | $K = 1$ | $K = 2$ | $K = 4$ | $s = 0{\cdot}1$ | $s = 0{\cdot}2$ | $s = 0{\cdot}4$ | $h = 2$ | $h = 4$ |
| $F = 0$ | | | | | | | | | |
| *P* | 0·08 | 0·11 | 0·15 | 0·19 | 0·21 | 0·33 | 0·51 | 0·22 | 0·43 |
| *T* | 11·92 | 9·51 | 7·54 | 5·96 | 9·64 | 8·87 | 7·14 | 8·63 | 7·15 |
| *SD* | 7·98 | 6·22 | 4·84 | 3·76 | 5·80 | 4·86 | 3·33 | 6·13 | 5·78 |
| $F = 0{\cdot}1$ | | | | | | | | | |
| *P* | 0·14 | 0·22 | 0·32 | 0·45 | 0·29 | 0·37 | 0·51 | 0·38 | 0·62 |
| *T* | 5·07 | 3·98 | 3·05 | 2·33 | 4·32 | 4·46 | 4·34 | 3·84 | 3·47 |
| *SD* | 4·07 | 3·06 | 2·21 | 1·56 | 3·18 | 3·12 | 2·71 | 3·09 | 2·89 |
| $F = 0{\cdot}5$ | | | | | | | | | |
| *P* | 0·19 | 0·31 | 0·48 | 0·67 | 0·36 | 0·41 | 0·51 | 0·53 | 0·78 |
| *T* | 2·29 | 1·97 | 1·64 | 1·36 | 2·05 | 2·12 | 2·19 | 1·84 | 1·63 |
| *SD* | 1·66 | 1·32 | 0·97 | 0·66 | 1·38 | 1·42 | 1·44 | 1·23 | 1·08 |

An increase in the number of examined progeny has a larger effect on increasing the proportion detected with partial inbreeding than with random mating (compare for example the increases in *P* from $K = 1$ to $K = 4$ for $F = 0$ and $F = 0{\cdot}5$). The proportional effect on time to detection is, however, approximately the same for all values of *F*. Values in Table 1 for $K = 0{\cdot}5$ would correspond, for example, to a case with *N* screened individuals and 50% reduction in viability of the mutant homozygote.

For $F = 0$, an increased selection coefficient for the mutant heterozygote enhances the chance of detection of the mutant, but the time to detection and its variance are little reduced (Robertson, 1978; Karlin & Tavaré, 1981*a*, *b*; see also Table 1). With partial inbreeding, the proportion detected is relatively less enhanced because, for large *s*, its value becomes independent of *F* (Table 1). The time to detection and its variance are little affected (even increased) with increasing *s* because, for large *F*, detection is essentially determined by inbreeding and selection merely delays detection by reducing the probability of loss.

An increase in the initial number of heterozygotes carriers (*h*), of course increases the proportion detected and reduces the time to detection and its variance. These effects are, however, proportionately less marked for larger values of *F*.

## 5. Discussion

Robertson (1978) and Karlin & Tavaré (1981*a*–*c*) obtained the distribution of the time to first detection as a homozygote of a recessive gene occurring only once in the initial generation, and found that this distribution had a nearly geometric form with a mean close to $2N^{\frac{1}{3}}$ for a wide range of *N*. These studies can be important in the detection of recessive deleterious visible mutants in experimental populations. They cannot be applied, however, to populations were mating is not completely at random, for example in plants subject to partial self-fertilization. This paper is intended to fill that gap. Simple expressions for calculating the probability of detection in recurrent generations for non-random mating populations are presented and shown to be very accurate unless both the proportion of inbred matings and the population size are very small.

Our results show that a relatively small proportion of inbred matings greatly increases the proportion detected and accelerates the average time to detection

Table 2. *Proportion detected (P), average time to detection (T) and its standard deviation (SD) for selfed (Sel) and full-sib (FS) lines as a function of K (the ratio of the number of examined to reproductive individuals times the viability of the recessive homozygote) (results from transition matrices; $s = 0$)*

| | Sel | | | FS | | |
|---|---|---|---|---|---|---|
| *K* | *P* | *T* | *SD* | *P* | *T* | *SD* |
| 1 | 0·50 | 2·00 | 1·41 | 0·35 | 4·00 | 2·37 |
| 2 | 0·70 | 1·60 | 0·96 | 0·43 | 3·44 | 1·83 |
| 4 | 0·87 | 1·27 | 0·34 | 0·48 | 3·12 | 1·52 |
| ∞ | 1·00 | 1·00 | 0·00 | 0·50 | 3·00 | 1·41 |

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relative to random mating, and this is more marked the higher is the population size. This reduction in the average time to detection is much larger than expected from merely applying the random mating approximation ($2N^{\frac{1}{3}}$) to the corresponding effective population size. An increase in the degree of inbreeding reduces the effective population size in proportion to $1/(1+F)$ (see Caballero & Hill, 1992), while the time to detection is approximately exponentially reduced.

Karlin & Tavaré (1981 *a*, *c*) reckoned that, starting with one heterozygote in a monoecious population of size $N$ with random mating, $0{\cdot}88N^2$ offspring should be examined to ensure that the probability of detection is at least one half. Thus, for say, $N = 100$, this means $K = 88$. With 19% selfing ($F = 0{\cdot}1$), the same objective is fulfilled with only $K = 5$, showing how powerful is a small proportion of inbreeding in screening for recessives.

If we are interested in early detection of recessive genes, the most extreme screening method is to subdivide the population into independent inbred lines. Table 2 gives results for selfed and full-sib lines. Our model for partial selfing with $F = 1$ would give slightly different results from those of selfed lines in Table 2 because, in our model, the number of progeny per individual is Poisson distributed and there are no independent lines. For example, for $K = 1$, $P$ is 0·34 and $T$ is 1·50, both somewhat smaller than with independent selfed lines (see Table 2). Note also that, because of the pair mating in the full-sib model, the proportion detected cannot be increased up to one by merely increasing $K$. In this paper, we have shown that early detection must not necessarily be confined to such large levels of subdivision. For example, if we had a dioecious population with $N = 100$, we would reduce $T$ by subdividing the population in couples, from 11·5 (with random mating and $K = 1$) to 4 (see Table 2). Without subdivision, to get nearly the same reduction, rather less than 50% of full-sibs matings would be necessary (and even less with larger $N$).

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## Appendix

Using expressions (2), the probability ($Pr^i[j_1, j_2]$) that one mating of type $i$ has $j_1$ $S$ mating and $j_2$ $D$ mating offspring is

$$Pr^S[j_1, j_2] = e^{-\mu_{SS}}(\mu_{SS}^{j_1}/j_1!)\, e^{-\mu_{SD}}(\mu_{SD}^{j_2}/j_2!)$$

and

$$Pr^D[j_1, j_2] = e^{-\mu_{DS}}(\mu_{DS}^{j_1}/j_1!)\, e^{-\mu_{DD}}(\mu_{DD}^{j_2}/j_2!),$$

with probability generating functions

$$G^S[\zeta, \gamma] = \sum_{j_1, j_2 = 0}^{\infty} Pr^S[j_1, j_2]\, \zeta^{j_1}\gamma^{j_2}$$

$$= \exp\{\mu_{SS}(\zeta - 1) + \mu_{SD}(\gamma - 1)\}$$

and

$$G^D[\zeta, \gamma] = \exp\{\mu_{DS}(\zeta - 1) + \mu_{DD}(\gamma - 1)\}.$$

Let $\Phi_t^i(\zeta, \gamma)$ be the generating function of the total number of progeny up to and including generation $t$, starting from a single mating of type $i$ in generation 0, then

$$\Phi_{t+1}^S(\zeta, \gamma) = \zeta G^S[\Phi_t^S(\zeta, \gamma), \Phi_t^D(\zeta, \gamma)]$$

$$= \zeta \exp\{\mu_{SS}(\Phi_t^S(\zeta, \gamma) - 1) + \mu_{SD}(\Phi_t^D(\zeta, \gamma) - 1)\} \quad (A\,1)$$

and

$$\Phi_{t+1}^D(\zeta, \gamma) = \gamma G^D[\Phi_t^S(\zeta, \gamma), \Phi_t^D(\zeta, \gamma)]$$

$$= \gamma \exp\{\mu_{DS}(\Phi_t^S(\zeta, \gamma) - 1) + \mu_{DD}(\Phi_t^D(\zeta, \gamma) - 1)\}.$$

In order to reduce these two equations into one, observe that

$$\frac{\Phi_{t+1}^S(\zeta, \gamma)}{\Phi_{t+1}^D(\zeta, \gamma)} = \frac{\zeta}{\gamma} \exp\{(x/4)(1 + s)[\Phi_t^S(\zeta, \gamma) - 1]\}.$$

Thus,

$$\Phi_t^D(\zeta,\gamma) = (\gamma/\zeta)\,\Phi_t^S(\zeta,\gamma) \times \exp\{(x/4)(1+s)[1-\Phi_{t-1}^S(\zeta,\gamma)]\}. \quad \text{(A 2)}$$

Substituting (A 2) into (A 1) gives a two-step recurrence relation for $\Phi_{t+1}^S(\zeta,\gamma)$. Now, the probability of no detection up to and including generation $t+1$ (starting from one $S$ mating) is

$$\Phi_{t+1}^S(1,\alpha) = G^S[\Phi_t^S(1,\alpha), \Phi_t^D(1,\alpha)],$$

where $\alpha$ is defined by (3). Substituting and denoting $\Phi_t^S(1,\alpha)$ as $\Phi_t$ for simplicity, gives eqn (4).



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