Size of population required for artificial selection

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SUMMARY

It is widely acknowledged that genetic drift is an important source of variation in response to artificial directional selection. How large should a selection line be in order to reduce the effect of genetic drift to an acceptably low level?

This paper investigates two criteria that can be used to answer this question in relation to short-term response to selection. The first criterion is coefficient of variation of response, and the second criterion is chance of success, where a successful selection programme is one in which the observed response is greater than a certain proportion, β, of expected response.

For a simple mass selection programme with intensity i and heritability h^2, the size of population required in order for the coefficient of variation of response to be γ after t generations, is approximately $2/(\gamma ih)^2 t$, and the size required for the chance of success to be α after t generations is approximately $2\{z_\alpha/(\beta-1)ih\}^2/t$, where z_α is the standard normal deviate corresponding to the probability α.

As an example, suppose it is required that after t generations the coefficient of variation of response be 10 % or that there be a 90 % chance of achieving at least 9/10 of expected response. Since $ih \leqslant 2$ in most selection programmes, the size of population required is at least $50/t$ or $82/t$ respectively. If $ih \leqslant 1$, the corresponding sizes are $200/t$ and $328/t$.

Results are extended to enable the calculation of size of population required for any type of artificial directional selection programme, including those in which generations overlap.

1. INTRODUCTION

The importance of population size in artificial selection programmes has been increasingly recognized in two different ways during the last 20 years. Firstly, and largely stemming from the work of Robertson (1960), it is now commonly recognized that artificial selection in small populations results in the chance loss of some desirable alleles, and hence leads to a decreased limit to selection. Secondly, it is now realized that in small populations genetic drift is a very important source of variation among selection lines, producing not only variation in mean response (Hill, 1971; Bohren, 1975) but also variation in within-line additive genetic variance (Bulmer, 1976; Avery & Hill, 1977).

However, despite the widely recognized importance of population size in artificial selection programmes, only one attempt has been made to answer the question so often asked in practice: how large should a population undergoing artificial selection be in order to reduce the effect of genetic drift to an acceptably low level?

Comstock (1974, 1977) answered this question in terms of the limit to selection, by solving for effective population size in the well-known chance-of-fixation equation developed by Kimura (1957) and applied to the problem of artificial selection by Robertson (1960). By assuming values for the size of allele effect and initial allele frequency, Comstock (1974, 1977) calculated the size of population required to ensure a certain probability of fixation of that allele. This approach is useful in providing an indication as to the minimum population size required in order to eventually capitalize on most of the genetic variance present in the base population. In practice, however, those who have to design artificial selection programmes, and those whose livelihoods depend on obtaining reasonable response in the short term, need a rather different approach: they need to know, for example, how large the population must be in order to give them a high probability of achieving at least a large proportion of the response predicted in the short term.

Fortunately, with the recent advances in our understanding of variation in response to artificial selection, as reviewed by Hill (1977a), it is now possible to provide an approximate answer to this question. In this paper, the general approach to calculating the size of population required for any particular artificial selection programme is outlined, and some general results are presented and discussed.

2. MODEL

Consider a selection line derived from a large base population and undergoing artificial directional selection with discrete generations for a quantitative character with heritability h^2, phenotypic variance σ_P^2, and additive genetic variance σ_A^2 ($= h^2\sigma_P^2$). Following Hill (1971), we assume that these parameters do not change during selection. Thus the model does not cover long term selection response. Assume initially that the population is monoecious, and that N individuals are selected as parents each generation from M individuals scored. A contemporaneous control line is maintained, with K individuals randomly chosen to be parents from J individuals scored. More general models incorporating overlapping generations, two sexes, divergent selection and lack of a control will be considered below.

Let $\bar{X}_t$ and $\bar{C}_t$ be the phenotypic means in the selection line and control line respectively, at generation t. Response to t generations of selection is then estimated as

$$\hat{R} = \bar{X}_t - \bar{C}_t. \tag{1}$$

Assuming no genotype–environment interaction between the selection line and its control, the variance of response is given by

$$\sigma_R^2 = \sigma_{dX}^2 + \sigma_{dC}^2 + \sigma_{eX}^2 + \sigma_{eC}^2, \tag{2}$$

where

σ_{dX}^2 = total drift variance in selection line,

σ_{dC}^2 = total drift variance in control line,

σ_{eX}^2 = measurement error variance in selection line,

σ_{eC}^2 = measurement error variance in control line.

Reviewing all previous work on variation in response to selection, Hill (1977*a*) concluded that the most appropriate value for σ_{dX}^2 is simply $t\sigma_A^2/N$, and it is well known that $\sigma_{dC}^2 = t\sigma_A^2/K$. These two expressions have the same form, but for very different reasons. The latter is the usual expression for drift variance in an unselected line. The former represents a compromise between a number of opposing factors (Robertson, 1977), including the effect of selecting parents that resemble each other much more closely than if chosen at random, which tends to decrease variance, and the effect of variance in within-line variance, which tends to increase variance. Being essentially an empirical compromise, the relationship $\sigma_{dX}^2 = t\sigma_A^2/N$ is certainly approximate. It has, however, provided a satisfactory description of variance in simulated selection lines (Robertson, 1977). The appropriate values for variance due to measurement error are σ_P^2/M and σ_P^2/J for the selection line and control line respectively. Substitution of these values into (2) gives

$$\sigma_R^2 \doteq t\sigma_A^2(1/N + 1/K) + \sigma_P^2(1/M + 1/J). \tag{3}$$

Now, the expected response to t generations of selection is

$$R = tih\sigma_A, \tag{4}$$

where i is the standardized selection differential. By assuming that phenotypic and genotypic values of individuals are bivariate normally distributed, we then have (Hill, 1971) that the observed response to selection ($\hat{R}$) is normally distributed with mean R and variance given by equation (3) above.

3. ANALYSIS

(i) *Criteria*

What criteria should be used in determining the size of population required for artificial selection? Of the many potential criteria, there are two that appear to be particularly useful.

(a) *Coefficient of variation*

The coefficient of variation is commonly used as a dimensionless measure of variability. In the present context, the expected coefficient of variation of response to selection, σ_R/R, can be evaluated from equations (3) and (4), for any selection programme in which J, K, M, N, i, h^2 and σ_P^2 are specified.

If the selection and control lines are the same size, both in numbers measured $(M = J)$ and numbers selected $(N = K)$, then, from equation (3),

$$\sigma_R^2 \doteq 2t\sigma_A^2/N + 2\sigma_P^2/M$$
$$\doteq 2\sigma_A^2(t + p/h^2)/N, \tag{5}$$

and the coefficient of variation is

$$\sigma_R/R \doteq \sqrt{[2(t + p/h^2)]}/tih\sqrt{N}, \tag{6}$$

where $p = N/M$ is the proportion selected. An even simpler expression for coefficient of variation can be obtained if p is small, or if t is not too small such that $t \gg p/h^2$, in which case

$$\sigma_R/R \doteq \sqrt{2}/ih\sqrt{(Nt)}. \tag{7}$$

It should be noted that the assumptions required in order to obtain (7) are equivalent to assuming that measurement error variance is negligible in comparison with drift variance. Equation (7) represents a lower limit of the coefficient of variation and hence, if anything, will lead to an over-optimistic view of the adequacy of a particular selection programme. On the other hand, if p is not small, and if t is sufficiently small such that $p \doteq th^2$, then $\sigma_R/R \doteq 2/ih\sqrt{(Nt)}$, which for most selection programmes will lead to an under-estimate of adequacy.

For either situation, we have the very simple result that the coefficient of variation of response to selection is determined solely by the parameter combination $ih\sqrt{(Nt)}$.

(b) Probability of success

We can define a successful selection programme as one in which the observed response is greater than a proportion β of expected response. The probability of success, then, is the probability of achieving an observed response greater than a proportion β of expected response. This will be our second criterion for deciding the size of population required for artificial selection.

Expressed algebraically, the probability of success is given by

$$\text{Prob}(\hat{R} > \beta R) = \text{Prob}\{(\hat{R} - R)/\sigma_R > (\beta - 1)R/\sigma_R\}$$
$$= \text{Prob}\{Z > (\beta - 1)R/\sigma_R\}, \tag{8}$$

where Z is a standard normal deviate. Thus the chance of success in a selection programme is a function of R/σ_R, which is the inverse of the coefficient of variation of response. From the previous section, it follows that the chance of success in a selection programme is a function of the parameter combination $ih\sqrt{(Nt)}$.

From expression (8) it can be seen that the probability of the observed response being greater than the expected response $(\beta = 1)$ is given by $\text{Prob}(Z > 0)$, which is 50%, as expected. When $\beta = 0$, the question becomes the quite interesting one of what is the chance that the observed response will be positive rather than negative? In other words, what is the probability of not going backwards?

(ii) *How large should a selection programme be?*

In its most general form (as in equation (3)), the value of σ_R^2, and hence the value of σ_R/R, depends among other things on J, K, M and N. For any model, M and J are functions of N and K respectively, being determined by the respective proportions selected. Thus for given proportions selected, there are really only two independent population size parameters, N and K. In order to answer the above question usefully, we have to reduce the number of independent population size parameters to one, by specifying a relationship between N and K. One such relationship often occurring in practice is that the number of parents in the selection and control lines is the same, in which case $N = K$.

As soon as σ_R/R can be expressed as a function of only one population size parameter (for example, N), we can ask what size of population is required, in terms of each of the criteria outlined above.

(a) *Coefficient of variation*

For this criterion, we shall ask the following question: what size of population is required in order to obtain a particular value of coefficient of variation of response, say γ. In this case, γ is chosen as being the largest acceptable value for the coefficient of variation of response to selection.

To answer this question, we want the value of N for which

$$\sigma_R/R = \gamma. \tag{9}$$

With the coefficient of variation as our criterion, the size of population required for artificial selection, S, is defined as the value of N that satisfies equation (9). Using the simple expression for σ_R/R as given in equation (7), we have

$$S \doteq 2/(\gamma i h)^2 t. \tag{10}$$

Since equation (7) represents a lower limit of coefficient of variation, equation (10) provides a lower limit to the size of population required. In other words, S as given by (10), represents the smallest possible size of any selection programme for which a coefficient of variation of γ could be expected. If, for example, a coefficient of variation of response of $\gamma = 10\%$ was thought to be adequate, and noting that $ih \leqslant 2$ in most selection programmes, then a population size of at least $50/t$ is required.

(b) *Probability of success*

Using our second criterion, the question now becomes the following: what size of population is required in order to obtain, with a probability α, an observed response that is greater than a proportion β of expected response?

To answer this question, we want the value of N which gives

$$\text{Prob}\,(\hat{R} > \beta R) = \alpha, \tag{11}$$

or, from (8),

$$\text{Prob}\,\{Z > (\beta-1)\,R/\sigma_R\} = \alpha. \tag{12}$$

It follows that the observed response will be greater than βR with a probability α, if the population size is such that

$$(\beta-1)\,R/\sigma_R = z_\alpha, \tag{13}$$

where z_α is the relevant tabulated value of the standard normal deviate.

The size of population required for successful artificial selection, S, is now defined as the value of N that satisfies equation (13).

Substitution of σ_R/R from equation (7) into equation (13) and solving for population size gives

$$S \doteqdot 2\{z_\alpha/(\beta-1)\,ih\}^2/t \tag{14}$$

as the size of population required for successful artificial selection, which, as for the previous criterion, is a minimum requirement.

Now, it could be argued that a reasonable criterion of success is to be 90 % certain ($\alpha = 0.9$) of achieving the objective, which gives $z_\alpha = 1.28$. And if the objective is to achieve at least 9/10 of the predicted response ($\beta = 0.9$), then the minimum size required is

$$S \doteqdot 328/t(ih)^2. \tag{15}$$

Since $ih \leqslant 2$ in most selection programmes, it follows that a population size of at least $82/t$ is required for there to be a 90 % chance of achieving 9/10 of the predicted response after t generations.

4. EXTENSION OF THE MODEL

(i) *Lack of a control*

Many selection programmes, especially those in commercial operations, are conducted without a control. It is therefore important to broaden our model to include such programmes.

In the absence of a control, it must be assumed that there is no environmental trend, and the potential importance of variance in common environmental effects among generations must be accounted for. Following Hill (1971, 1972b), we assume that effects common to individuals within a generation are randomly and independently distributed among generations, with mean zero and variance σ_c^2. This variance in common environmental effects is another source of error variance in the selection line, so that we now have $\sigma_{eX}^2 = \sigma_P^2/M + \sigma_c^2$, with drift variance remaining unaltered as $t\sigma_A^2/N$. In the absence of a control, the observed response is

$$\hat{R} = \bar{X}_t - \bar{X}_0 \tag{16}$$

with expected variance

$$\sigma_R^2 = \sigma_{dX}^2 + 2\sigma_{eX}^2. \tag{17}$$

Substituting the above values for σ_{dX}^2 and σ_{eX}^2 into (17), and recalling that $M = N/p$, we have

$$\sigma_R^2 \doteqdot \sigma_A^2(t + 2p/h^2)/N + 2\sigma_c^2. \tag{18}$$

By comparing equations (5) and (18) it can be seen that the difference in variance of response between a selection programme with a control and one without a control is $t\sigma_A^2/N - 2\sigma_c^2 = \sigma_{dX}^2 - 2\sigma_c^2$. Thus, if the common environmental variance is one-half the drift variance, then the variance of response is similar with or

without a control. If σ_c^2 is greater than half the drift variance, then variance of response is smaller with than without a control; if σ_c^2 is less than half the drift variance, then variance of response is larger with than without a control.

What values of σ_c^2 are likely to be met in practice? While few values of this parameter are available in the literature, it is now possible (Hill, 1972*b*) to estimate σ_c^2 from selection experiments quite simply. Once such a value has been determined, then appropriate adjustments can be made where necessary to the conclusions drawn from the model involving a control line.

For example, if σ_c^2 is larger than half the drift variance, the chance of success of a particular selection programme will be less in the absence of a control, and vice versa. Similarly, if σ_c^2 is larger than half the drift variance, the size of population required will be larger than if a control were maintained, and vice versa.

(ii) *Divergent selection*

An alternative programme to the one described in the basic model is to conduct selection for the same character in opposite directions in two lines. This form of selection was discussed extensively by Hill (1972*a*). Letting $\bar{X}_{u,t}$ and $\bar{X}_{d,t}$ represent the phenotypic means of the up and down selection lines respectively, at generation t we have

$$\hat{R} = \bar{X}_{u,t} - \bar{X}_{d,t}, \tag{19}$$

$$\sigma_R^2 = 2\sigma_{dX}^2 + 2\sigma_{eX}^2, \tag{20}$$

and if there is no asymmetry,

$$R = 2tih\sigma_A. \tag{21}$$

If N individuals are selected from M scored each generation in each line, with $N = pM$ as before, then

$$\sigma_R^2 \doteq 2\sigma_A^2(t+p/h^2)/N \tag{22}$$

as in equation (5) for the basic model. Thus

$$\sigma_R/R \doteq \sqrt{(t+p/h^2)}/tih\sqrt{(2N)}, \tag{23}$$

which is one half the coefficient of variation for one selection line and a control (equation (6)). Thus divergent selection is much more efficient than using one selection line and a control, and the size of population required to satisfy a given criterion is correspondingly lower. If, however, the comparison is between divergent selection, and unidirectional selection without a control, then if $\sigma_c^2 = 0$ and if the same total number of parents are selected in each case, divergent selection results in a doubling of response and a quadrupling of variance of response (Hill, 1978), in which case coefficient of variation and hence the overall requirement in relation to the number of individuals selected per generation remains the same under both types of selection programmes.

(iii) *Two sexes*

In the most general case, the existence of two sexes involves four pathways by which gametes can pass from parents to offspring (male to male, male to female,

female to male and female to female), with expected response to t generations of selection given by

$$R = t\bar{G}\sigma_A, \tag{24}$$

where $\bar{G}$ is the average genetic superiority, in units of σ_A, of those individuals selected as parents. In its most general form,

$$\bar{G} = \left(\sum_{j=1}^{4} i_j \rho_j\right)/4,$$

where i_j and ρ_j are respectively the intensity and the accuracy of selection for the jth pathway. If accuracy of selection ρ_j is defined in the usual way as the correlation between the criterion of selection and true breeding value, then equation (24) is a completely general prediction of response to selection, incorporating the whole range of possibilities from simple mass selection in both sexes, through to selection for a sex-limited character and/or the use of any type of selection index. With two sexes, drift variance in the selection line is now $t\sigma_A^2/N_e$, where N_e is effective population size. If N_m males and N_f females are selected as parents each generation, then as usual, $1/N_e = 1/4N_m + 1/4N_f$. And if M_m males and M_f females are scored each generation in the selection line, then the measurement error variance is simply the variance of the average of observations on males and females, which is σ_P^2/M_e, where $1/M_e = 1/4M_m + 1/4M_f$. In the same way, drift variance and error variance in the control line can be written as $t\sigma_A^2/K_e$ and σ_P^2/J_e respectively. Substitution of these values into equation (2) gives variance of response, and combining this with equation (24) gives

$$\sigma_R/R \doteq \sqrt{[t(1/N_e + 1/K_e) + (1/M_e + 1/J_e)/h^2]}/t\bar{G} \tag{25}$$

in its most general form.

With the basic model we saw that a simple and yet useful expression for the size of population required can be obtained by assuming that error variance is negligible in comparison to drift variance and that the selection and control lines are the same size. With two sexes this gives

$$\sigma_R/R \doteq \sqrt{(2)}/\bar{G}\sqrt{(N_e t)}, \tag{26}$$

which when substituted into equations (9) and (13) leads to

$$S_e \doteq 2/(\gamma\bar{G})^2 t \tag{27}$$

and

$$S_e \doteq 2\{z_\alpha/(\beta-1)\bar{G}\}^2/t \tag{28}$$

as the minimum effective population size required in relation to coefficient of variation and chance of success respectively. Since equations (26), (27) and (28) are analogous to those obtained with the basic monoecious model (equations (7), (10) and (14)) the generalizations described for that model apply equally well to the dioecious model.

The size of a selection line is often specified in terms of the number of breeding males and/or females in the line at any one time. It would be useful, therefore, if

values for these parameters could be obtained from S_e. Fortunately, with discrete generations and two sexes, this is a simple task for the most common situation encountered, namely where the four pathways reduce to two (males to offspring, and females to offspring). If x females are mated to each male in this situation, then in general $N_e \doteq 4xN_m/(1+x)$, where, as before, N_m is the number of male parents used each generation. The required size of the selection line in terms of breeding males is then

$$S_m \doteq S_e(1+x)/4x, \tag{29}$$

where S_e is obtained from equations (27) or (28). As a special case of a well-known relationship, if selection is much more intense in males than in females so that x is very large, then S_m is approximately one-quarter of S_e.

In terms of breeding females, the required size is

$$S_f = xS_m. \tag{30}$$

It is worth noting that if equal numbers of each sex are scored ($M_m = M_f$), then $x = p_f/p_m$, where p_f and p_m are the proportions selected of females and males respectively.

(iv) *Overlapping generations and two sexes*

Extension of the model to include overlapping generations is essential from a practical point of view, but involves more restrictions than the previous extensions. The problem is that the simple expressions for expected response and for drift variance apply only asymptotically in the case of overlapping generations (Hill, 1977b; Johnson, 1977). Thus the extension to overlapping generations described below is not valid for the first few time units (hereafter called years) of a selection programme. Other assumptions that are necessary for a valid extension to over-lapping generations are that the number of individuals entering the selection line as parents each year, the age distribution of individuals within the line, and the age distribution of parents of individuals born in any year are all fairly constant. If these conditions are met, then the values for N_e and K_e are determined in exactly the same way as described in the previous section (Hill, 1972c).

Reverting to the original model of a selection line and a control, and following Hill (1972c), the drift variance per year in the selection line is $\sigma_A^2/N_e\bar{L}$ and in the control line is $\sigma_A^2/K_e\bar{L}$, where $\bar{L}$ is the average generation interval, defined as the average age of parents when their offspring are born. In its most general form

$$\bar{L} = \left(\sum_{j=1}^{4} L_j\right)/4,$$

where L_j is the generation interval for the jth pathway. For simplicity, it is assumed that $\bar{L}$ is the same in the selection and control lines. It is obvious that the error variances in the selection line and the control are the same for both discrete and overlapping generations, since estimates of phenotypic means have to be made in the same manner in either situation. Thus we now have $\sigma_{dX}^2 = t\sigma_A^2/N_e\bar{L}$, $\sigma_{dC}^2 = t\sigma_A^2/K_e\bar{L}$, $\sigma_{eX}^2 = \sigma_P^2/M_e$ and $\sigma_{eC}^2 = \sigma_P^2/J_e$, which can be substituted directly

into equation (2) to obtain the variance of response, noting that t is now the number of years of selection.

Providing that care is taken in defining the various parameters in relation to age structure (see, for example, James, 1977a), expected response to t years of selection can be written as

$$R = t\sigma_A \bar{G}/\bar{L}, \tag{31}$$

in which case the most general expression for σ_R/R becomes

$$\sigma_R/R \doteqdot \bar{L}\sqrt{[(1/N_e + 1/K_e)t/\bar{L} + (1/M_e + 1/J_e)/h^2]/t\bar{G}}. \tag{32}$$

Again, as in the previous section, we can obtain very simple expressions for effective size of population required, if $t \gg p/h^2$ or more specifically if measurement error variance is negligible in comparison with drift variance, and by considering the situation where both the selection line and its control are of the same size. In this case, equation (32) reduces to

$$\sigma_R/R \doteqdot \sqrt{(2\bar{L})}/\bar{G}\sqrt{(N_e t)}, \tag{33}$$

which after substitution into equations (9) and (13) gives

$$S_e \doteqdot 2\bar{L}/(\gamma\bar{G})^2 t \tag{34}$$

and

$$S_e \doteqdot 2\{z_\alpha/(\beta-1)\,\bar{G}\}^2\,\bar{L}/t \tag{35}$$

as the minimum effective size of population required. It should be noted that the above values of σ_R/R and S_e are the same as those for discrete generations (equations (26), (27) and (28)), with $t/\bar{L}$ in place of t. Since the generation interval usually consists of at least several time periods in selection programmes with overlapping generations, the assumption of negligible measurement error variance in relation to drift variance is less valid here than for the case of discrete generations. Thus the coefficient of variation of response in equation (33) is likely to be more of an under-estimate than its discrete generation counterpart in equation (7), and the sizes of population required, as given in equations (34) and (35), are also more likely to be underestimates, especially when t is small. In using these equations in the design of selection programmes, therefore, it should be remembered that the sizes of population obtained from equations (34) and (35) are absolute minima.

As with discrete generation programmes, the size of selection lines where generations overlap is often described in terms of the total number of breeding males and/or females in use at any time. In order to discuss these parameters where generations overlap, it is convenient to consider the two-pathway and four-pathway situations separately.

(a) Two pathways

With overlapping generations, we need to specify not only the mating ratio (x), but also the replacement rate for males (r_m) and females (r_f), where replacement rate is the proportion of breeding individuals of the relevant sex that are replaced each year. If m males and f females enter the selection line as parents each year,

then the total numbers of male and female parents are m/r_m and f/r_f, respectively. With a mating ratio of x, this gives $f/r_f = xm/r_m$. Now in general, $N_e \doteq 4N_m N_f/(N_m + N_f)$, where, as before, N_m and N_f are the numbers of males and females respectively entering the population each generation. If deaths and culling after entry to the breeding population are negligible, then $N_m = m\bar{L}$ and $N_f = f\bar{L}$. Substitution of the relevant values, and solving in relation to the particular case being considered in this paper leads to

$$S_m \doteq S_e(r_m + xr_f)/4xr_m r_f \bar{L} \tag{36}$$

as the size of population in terms of breeding males required for successful artificial selection, with S_e being evaluated from equations (34) or (35). For females, we then have

$$S_f = xS_m. \tag{37}$$

If equal numbers of males and females are scored, and if p_m and p_f are the respective proportions selected, then $x = (p_f r_m)/(p_m r_f)$. It should be noted that if selection is much more intense on males than on females so that x is large, then S_m is approximately $S_e/4r_m\bar{L}$.

(b) *Four pathways*

Although there is no simple relationship between effective population size and the numbers of breeding males and females for the four-pathway situation, a useful approximation is $N_e \doteq 16N_{mm}N_{mf}/(3N_{mm} + N_{mf})$, as given by Robertson (1954), where N_{mm} and N_{mf} are the numbers of males that enter the population each generation to produce respectively male and female offspring. Because this approximation involves the assumption of negligible differential selection within subgroups of the population, it tends to give an over-estimate of the true N_e (James, 1978). If m_m and m_f are the corresponding numbers of male parents entering the population each year, and if deaths and culling after entry to the breeding population are negligible, then $N_{mm} = m_m\bar{L}$ and $N_{mf} = m_f\bar{L}$. Furthermore, if r_{mm} and r_{mf} are the respective replacement rates, then the actual numbers of males in use at any one time are m_m/r_{mm} to breed males, and m_f/r_{mf} to breed females, with the latter also being the total number of males in use at any one time. If the ratio of males breeding females to males breeding males is y, then after substitution and rearrangement we obtain

$$S_{mm} \doteq S_e(3r_{mm} + yr_{mf})/16yr_{mm}r_{mf}\bar{L} \tag{38}$$

as the size of population in terms of males to breed males required for successful artificial selection, with S_e given as before by equations (34) or (35). The total number of breeding males is then given by

$$S_{mf} = yS_{mm}. \tag{39}$$

(v) *Open nucleus breeding schemes*

The general theory of open nucleus breeding schemes has been developed by James (1977*b*), Hopkins & James (1978) and James (1978). In the course of this

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work, very generalized expressions for response and variance of response were obtained. Thus it is now possible to calculate the coefficient of variation of response and hence the chance of success of any open nucleus breeding scheme. Unfortunately, the expression for coefficient of variation can not be simplified to the extent required to obtain a simple expression for the size of population required. Resort must be made, therefore, to numerical solution of equations (9) or (13) in order to determine the size required for an open nucleus breeding scheme.

5. RESULTS

(i) *Criteria*

The coefficient of variation of response to artificial selection is shown in Fig. 1 as a function of $ih\sqrt{(N_e t)}$, while Fig. 2 illustrates the chance of achieving an
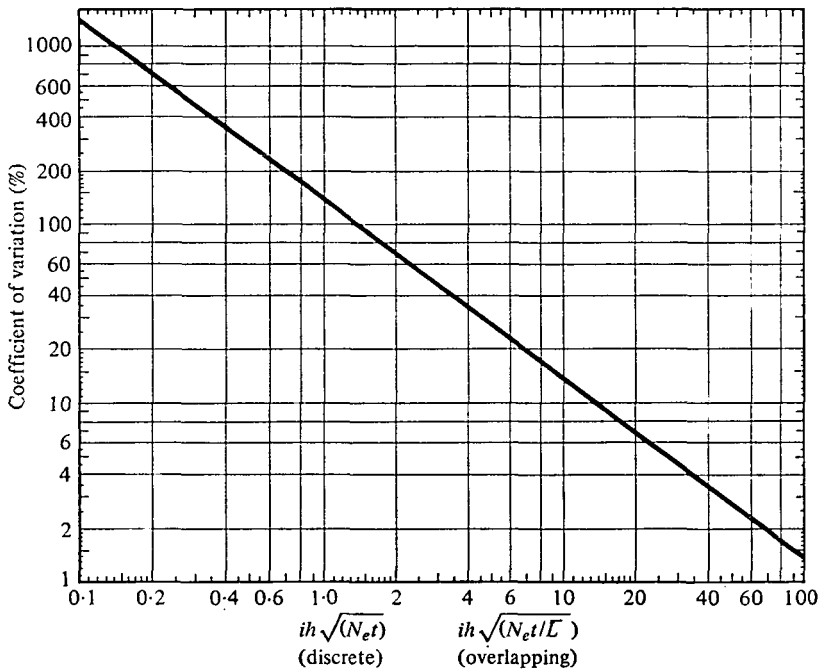

Fig. 1. Coefficient of variation of response to directional selection with intensity i and heritability h^2 in a population with effective size N_e, where selection is conducted for t discrete generations, or for t time units in a population with overlapping generations in which average generation interval is $\bar{L}$ time units. To obtain coefficient of variation for selection on a sex-limited character and/or on any index, replace ih with $\bar{G} = (\Sigma_{j=1}^{4} i_j \rho_j)/4$.

observed response $(\hat{R})$ greater than various proportions of expected response (R), also as a function of $ih\sqrt{(N_e t)}$. Fig. 1 was obtained directly from equation (26), and the curves in Fig. 2 were obtained by substituting the value of σ_R/R from
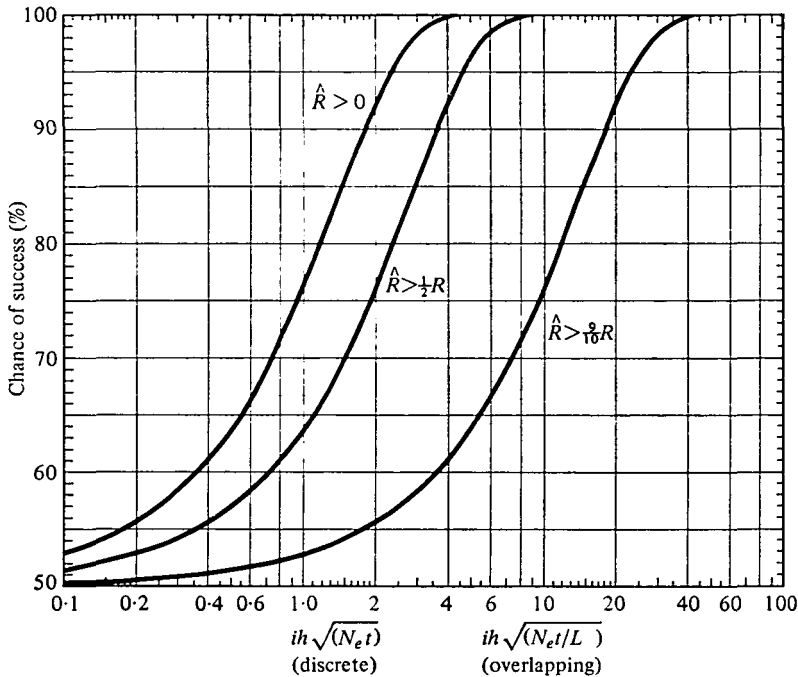
Fig. 2. Chance of success in a directional selection programme with selection intensity i and heritability h^2 in a population with effective size N_e. Chance of success is given for t discrete generations of selection, and for t time units of selection in a population with overlapping generations in which average generation interval is $\bar{L}$ time units. To estimate chance of success for selection on a sex-limited character and/or on any index, replace ih with $\bar{G} = (\Sigma_{j=1}^{4} i_j \rho_j)/4$. Curves are drawn for $\beta = 0$, $\frac{1}{2}$ and $9/10$.

equation (26) into equation (8), for the general case of mass selection for a character that can be scored in both sexes ($\bar{G} = ih$). These figures also illustrate the co-efficient of variation, or the chance of success after t time units of selection with overlapping generations, as a function of $ih\sqrt{(N_e t/\bar{L})}$, from equations (33) and (8).

To illustrate the general conclusions that can be drawn from Figs. 1 and 2, consider response to one generation or one time period of selection ($t = 1$). Note that the limitation of the theory in relation to overlapping generations, as described earlier, does not preclude consideration of one time-period of selection, so long as that time period does not occur right at the beginning of the selection programme. Most discrete generation selection programmes have values of $ih\sqrt{(N_e t)}$ somewhere between 1 and 10 if $t = 1$. It can thus be seen from Fig. 1 that such programmes have a coefficient of variation of response between approximately 140 % and 14 %. It can also be seen, from Fig. 2, that such programmes have at least a 76 % chance of resulting in some improvement (as distinct from going backwards). At the same time, however, such programmes have less than a 76 % chance of achieving 9/10 of the predicted response. For programmes with overlapping generations and where time is measured in years, the value of $ih\sqrt{(N_e t/\bar{L})}$ often lies within the range 1–5 if $t = 1$, in which case the coefficient of

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variation lies between 140% and 28%. The chance of making at least some improvement in one year is at least 76%, but the chance of achieving 9/10 of expected response in one year is less than 64%.

(ii) *How large should a selection programme be?*

In order to cater for as many different types of selection programmes as possible, this question has been answered in terms of effective population size (S_e), and the size of population in terms of total breeding males (S_m) where selection is much more intense on males than on females. In this situation, as we have seen, S_m is approximately $S_e/4$ with discrete generations, and $S_e/4r_m\bar{L}$ with overlapping generations.
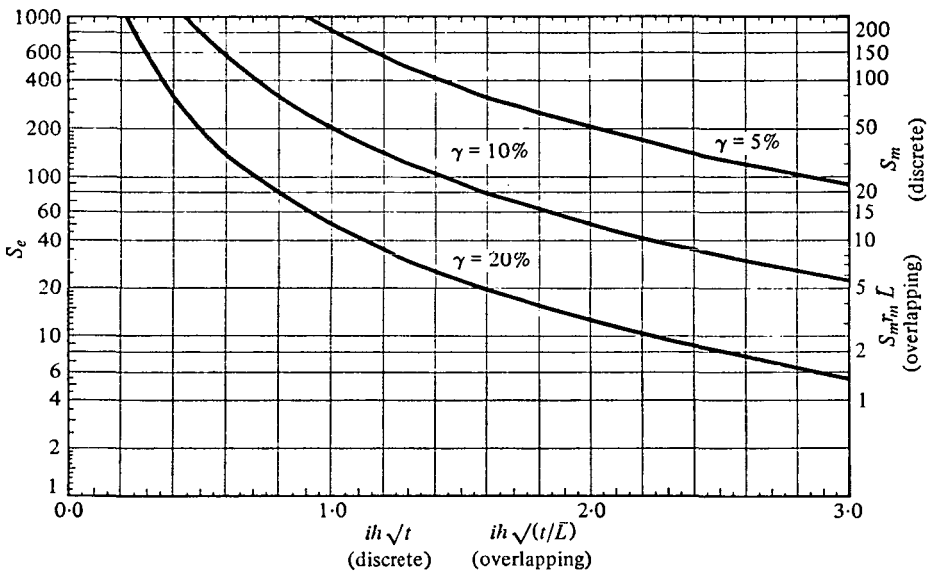

Fig. 3. Effective population size required (S_e) and total number of breeding males required (S_m) in order to obtain a coefficient of variation of selection response (γ) equal to 5%, 10% and 20%, for selection with intensity i and heritability h^2. S_e and S_m are given for t discrete generations, and for t time units with overlapping generations in which average generation interval is $\bar{L}$ time units. To obtain S_e and S_m for selection on a sex-limited character and/or on any index, replace ih with $\bar{G} = (\Sigma_{j-1}^4 i_j\rho_j)/4$.

The results for these measures of population size are illustrated in Fig. 3, in terms of coefficient of variation, and in Fig. 4, in relation to ensuring a 90% chance of the observed response ($\hat{R}$) being greater than various proportions of the expected response (R). Values of S_e were obtained from equations (27) and (28) with discrete generations, and from equations (34) and (35) with overlapping generations, in each case assuming mass selection for a character that can be measured in both sexes ($\bar{G} = ih$). The values on the right hand side of Fig. 3 and 4 are simply $S_e/4$, and so correspond approximately to S_m for discrete generations, and to $S_m r_m\bar{L}$ for overlapping generations. It is evident that in order to be fairly
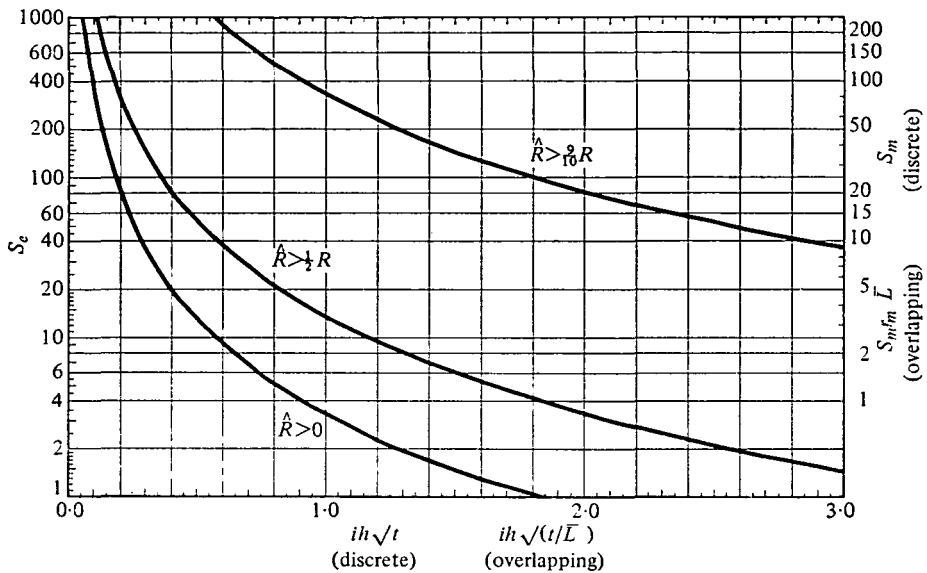
Fig. 4. Effective population size required (S_e) and total number of breeding males required (S_m) in order to have a 90 % chance of achieving the proportions $\beta = 0$, $\frac{1}{2}$ and 9/10 of expected response to mass selection with intensity i and heritability h^2. S_e and S_m are given for t discrete generations, and for t time units with overlapping generations in which average generation interval is $\bar{L}$ time units. To estimate S_e and S_m for selection on a sex-limited character and/or on any index, replace ih with $\bar{G} = (\Sigma_{j=1}^4 i_j \rho_j)/4$.

certain that observed response will be quite close to expected response over a small number of generations or years, quite a large population is required. For example, if the top 10 % of individuals are selected for a character with a heritability of 0·3, then ih is approximately 1, in which case an effective population size of approximately 200 is required for the coefficient of variation of response to be 10 %, and an effective population size of approximately 330 is needed to ensure a 90 % chance of achieving 9/10 of the expected response to one generation of selection $(t = 1)$.

6. DISCUSSION

There are several different approaches that can be taken in planning selection programmes. The one used in this paper involves designing the programme so as to maximize response per generation or per unit of time, in the latter case along the lines suggested by Ollivier (1974). Having done this, the question then is how large does the population have to be in order to satisfy specific requirements in relation to coefficient of variation or chance of success. This approach is most relevant to commercial programmes, and to any experimental programme in which the aim is to maximize response. For example, the aim may be to obtain the largest possible difference between a selection line and a control as quickly as possible.

If, however, the aim is to compare two or more selection strategies and if the total facilities are limited, then a different approach can be taken. Suppose, for example, there is a restriction on the number of individuals that can be measured. In this case, the smaller the proportion selected, the greater the expected response, but also the greater the variance of response. Combining these two effects together, the coefficient of variation of response increases as the proportion selected approaches both zero and one, for a given number of individuals measured. Clearly there is an optimum value of proportion selected for which the coefficient of variation of response is a minimum (Soller & Genizi, 1967). In planning a selection programme along these lines, the power of the experiment and hence its ability to differentiate between various strategies, is maximized for a given amount of work done.

It could be, however, that the minimum coefficient of variation so calculated is too high, or the corresponding chance of success may be unacceptably low, in which case it would be best not to proceed with the programme until further facilities can be found.

(i) *The choice of values for the criteria*

This raises the question as to what are acceptable values for the coefficient of variation, and, in relation to chance of success, what are acceptable values of α and β?

There may be some situations in which quite high values of γ, or low values of α and β will be sufficient. There are many situations, however, where the reverse will apply.

Consider, for example, a selection programme in which the aim is to use a single herd, flock or population to demonstrate the desirable effects of selection to the members of a breed society; or a programme for a herd, flock or population belonging to a commercial breeding company, in which the board of directors will tend to judge the merit (and hence future employment prospects) of their geneticist according to the response actually observed from year to year; or a student research project involving a selection programme in which the supervisor needs to be quite certain, for example 90 % certain, that after a limited (and usually short) period of time, the student will have obtained the desired difference between a selection line and its control.

In all these situations, the selection programme would have been designed so as to maximize expected response ($\sigma_A \bar{G}$, or $\sigma_A \bar{G}/\bar{L}$). But the breed society, the board of directors and the student will not be impressed if they fail to actually observe a response that is fairly close to that predicted. And although theoretically it is often sufficient to invoke chance variation due to small population size as the reason for a large and unfavourable discrepancy between expected and observed response, this explanation provides very little comfort to those who have devoted considerable effort and expense to a selection programme which they may be unable, or unwilling, to repeat. Thus there will be many situations in the laboratory and in the field where γ should be low, and where both α and β need to be high.

(ii) *Practical examples*

In order to illustrate the application of the results obtained in this paper, let us consider some particular selection programmes. A typical *Drosophila* programme, for example, might involve discrete generations with the top 5 out of 25 in each sex being selected for a character with heritability of 0·4. If there is a control of similar size, then we have $N_e = K_e = 10$, $M_e = J_e = 50$, $h^2 = 0.4$, $p = 20\%$ leading to $i = 1.4$, and hence $\bar{G} = ih = 0.89$. If this were a student project which was to run for 10 generations ($t = 10$), then we have from equation (25) a coefficient of variation, σ_R/R, of 16%. The chance of observing at least 9/10 of expected response after 10 generations is, from equation (8),

$$\text{Prob}\{Z > (0.9 - 1.0)\, 6.1\} = \text{Prob}(Z > -0.61),$$

which when read from appropriate tables of the standard normal deviate, is 73%. Had we used Figs. 1 and 2 (derived from equation (26)) in order to obtain approximate and, if anything, over-optimistic answers, then $ih\sqrt{(N_e t)}$ is 8·9 for $t = 10$ which, from the graphs gives a coefficient of variation of approximately 16%, and a chance of success of approximately 74%. Thus for this particular example, and for many others that have been tested, the approximate coefficient of variation and chance of success as obtained from Figs. 1 and 2 are sufficiently accurate to be quite useful.

To illustrate the determination of size of population required, consider a typical beef cattle selection programme of the type discussed by Hill (1977b), which involves two pathways with overlapping generations. In this programme the top 7% of bulls ($p_m = 0.07$) and all cows ($p_f = 1$) are selected as parents, giving 1·9 and zero as the respective values of i, and the character being selected has $h^2 = 0.4$. This gives $ih = \{(1.9 + 0)/2\}0.63 = 0.6$. If the aim of this selection programme is to illustrate to breeders what can be achieved over a ten year period, then $t = 10$ and since average generation interval is 2·5 years, $ih\sqrt{(t/\bar{L})} = 1.2$. As this selection programme is largely a public relations exercise, it is not worth doing unless, for example, there is a high probability that the observed results will be quite close to the predicted results, such that both α and β equal 0·9. From Fig. 4 it can be seen that these values require an S_e of approximately 230 and hence a value of $S_m r_m \bar{L}$ approximately equal to 57. Since all bulls and one-third of the cows are replaced each year ($r_m = 1$, $r_f = 1/3$), the size of herd required is $S_m = (S_m r_m \bar{L})/r_m \bar{L} = 57/(1 \times 2.5) = 23$ bulls and $S_f = xS_m = \{(p_f r_m)/(p_m r_f)\}S_m = 42.9 \times 23 = 987$ cows.

(iii) *Replication*

For any total fixed number of individuals that can be scored, the variance of response in one selection line of size N is the same as the variance of mean response in n lines each of size N/n (Hill, 1971). Thus, for a given total size of facilities available, the answers obtained in this paper apply equally to response to selection in one line, or to average response to selection in several proportionately smaller lines.

Although the opportunity for replication in many large animal selection programmes is usually very limited, laboratory experiments are often replicated. The theory developed in this paper can be used to determine the number of replicates required to bring the coefficient of variation down, or the chance of success up to a particular level. Consider, for example, the *Drosophila* research project discussed above. How many replicates of size $N_e = 10$ would the student require in order to provide a 90 % chance of the average response being 9/10 of that predicted over 10 generations? With $ih = 0.89$ and $t = 10$ we have $ih\sqrt{t} = 2.81$ for which, from Fig. 4, it can be seen that the effective population size required is approximately 40, which means that 4 replicates each of size $N_e = 10$ would be required.

(iv) *Inbreeding depression*

Throughout this paper, the effect of inbreeding depression on expected response has been ignored. To what extent will inbreeding depression alter the conclusions reached? If inbreeding depression reduces expected response by a fraction b, then the coefficient of variation of response is increased from σ_R/R to $\sigma_R/R(1-b)$ and the chance of success is decreased to Prob $\{Z > (\beta-1)\ (1-b)\ R/\sigma_R\}$. In order to illustrate the effect of inbreeding depression, it is convenient to express R and inbreeding depression as a percentage of the original population mean. Suppose, for example, that R is 3 % per generation, and that inbreeding depression occurs at the rate of 0.5 % per 1 % ΔF, where ΔF is the increase in average inbreeding coefficient per generation. If $\Delta F = 1$ % in this programme, then expected response is reduced from 3 % to 2.5 % per generation, a reduction of one-sixth. Thus $b = 1/6$, in which case the coefficient of variation is 1.2 times greater than in the absence of inbreeding depression. If σ_R/R was originally 15 %, then it is increased to 18 %, and the chance of observing at least 90 % of expected response is decreased from 75 % to 71 %. In this way it is relatively easy to quantify the effect of inbreeding depression on coefficient of variation and chance of success.

It is much more difficult, unfortunately, to calculate the size of population required. In order to do this, the reduction in expected response has to be expressed in terms of the effective population size so that expected response becomes approximately $tih\sigma_A - 100It/2N$, where I is inbreeding depression expressed in units of the character being selected, per 1 % ΔF, and where the programme is sufficiently short-term such that ΔF is approximately $t/2N$. Thus the denominator of the expression for coefficient of variation now contains two terms, and no simple algebraic expression for size of population required can be obtained. It would be possible, however, to solve equations (9) or (13) numerically in order to determine the appropriate size for a particular programme.

(v) *Another measure of size required*

It is obvious that the results of this study apply only to relatively short-term selection response, before the values of h^2 and/or σ_P are altered by selection. This being so, it is of interest to compare the results obtained here with those obtained by Comstock (1974, 1977), who, as mentioned earlier, was concerned with the size

of population required to provide a high chance of ultimately fixing most favourable alleles. An important difference between Comstock's long-term criterion and the short-term criteria discussed in this paper is that the size required in relation to the former is inversely proportional to the frequency and to the size of the effect of individual alleles. In comparison, these factors are relevant to the short-term criteria only in so far as they affect additive genetic variance.

How different are the requirements for short-term and long-term selection? In order to provide a 90 % chance of fixing alleles with an effect on the population mean of at least 1 % and with an initial frequency as low as 0·1, Comstock showed that a population size of 230 was required. If one was content to fix only genes of larger effect (2 % of the mean) with a higher initial frequency (0·2), then the number required was reduced to approximately 60. In the present study, it was concluded that the absolute minimum population size required in order to provide a 90 % chance of observing at least 9/10 of the expected response after t generations is $82/t$. For many programmes, where $ih \leqslant 1$, the absolute minimum is much higher, at approximately $300/t$.

Thus it appears that the minimum population size required to give a high chance of observing a large proportion of response to one generation of selection ($t = 1$) is of the same order as that required to give a high chance of ultimately fixing a reasonable proportion of useful genes. However, the size of population required in relation to the short-term criteria is indirectly proportional to t, so that, for example, the size required for a quite satisfactory short-term programme lasting five generations is approximately one-fifth of that required to satisfy the long-term criterion. Thus, the selection programmes most likely to be large enough to eventually retain most of the available useful genes are those that have to be evaluated every generation or every year. To the extent that frequent evaluation occurs in commercial selection programmes, those commercial programmes that satisfy the appropriate criteria as described in this paper are likely to be large enough to satisfy the long-term criteria as well. Consequently, there may be less conflict than is generally assumed between short-term and long-term aims in a well-designed commercial selection programme.

(vi) *Sources of error*

Various approximations have been used throughout this study. Not the least of these were setting drift variance in a selection line equal to $t\sigma_A^2/N$, and assuming that measurement error variance is negligible in comparison with drift variance. In addition, implicit throughout this study is the assumption that parameters such as heritability are known without error, and that there is no variance in i, the standardized selection differential. The use of these and other assumptions and approximations means that the results obtained are approximate. They do, however, provide general guidelines as to the size of population required in artificial selection programmes. To the extent that measurement error variance is not negligible, especially when programmes are to be evaluated at short intervals, the guidelines should be viewed as minimum requirements.

(vii) *Conclusion*

The present study has examined the coefficient of variation, the chance of success, and the population size required in relation to the short-term of an artificial selection programme. In so doing, it has not been concerned with methods of maximizing short-term response, but rather with the size of population required once the optimum design in relation to maximizing short-term response has been determined.

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