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Theory of Nucleus Breeding Schemes with Overlapping Generations

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Summary. Explicit methods are derived for estimating steady-state genetic responses and genetic differences between nucleus and base progeny crops in open nucleus breeding schemes which utilize genetic differences between progeny groups with parents of different ages or between age groups. Explicit methods are also given for estimating proportions which should be selected from the different nucleus and base selection groups so as to maximise genetic responses under each of a range of selection methods. Some basic differences between selection programmes utilizing genetic differences between progeny groups with parents of different ages and those utilizing genetic differences between age groups in nucleus breeding schemes are summarized.

Key words: Nucleus – Genetic – Breeding – Overlapping generations

Introduction

The theory of open nucleus breeding schemes has been discussed by Jackson and Turner (1972), Rae (1974), Clarke (1975) and James (1977b). In none of these papers were allowances made for genetic differences between progeny groups from parents of different ages. Bichard, Pease, Swales and Özkütük (1973) and Hopkins and James (1977) have shown how such allowances can be made when selecting in a single layer. Hopkins and James distinguished 'progeny selection', in which selection is made at a single stage and, except for deaths, all selected animals are used for breeding for the same length of time, from 'parent selection', in which animals remain in the breeding population for varying lengths of time, a particular age group being subject to culling several times during its life. Thus in 'progeny selection' only one progeny crop is subjected to selection in any one year while in 'parent selection' all potential parents are subjected to selection every year.

Although James (1977b) gave general equations for the annual rate of genetic gain (G) and the difference between mean breeding values of nucleus and base progeny crops (A), the application of his general equations to open nucleus breeding schemes which utilize genetic differences between parental age subgroups or between age groups is not immediately obvious. Further, in the examples given by James (1976) to illustrate the use of this equations, no allowance was made for such genetic differences. In this paper we show explicitly how selection of arbitrary proportions from different parental age subgroups (progeny selection) or from groups of animals of different ages (parent selection) can be accommodated in expressions for G and A. The equations for progeny selection are given in a modified form more suitable for computation. We also define criteria for estimating the proportions which should be selected from the different nucleus and base selection groups so as to maximise genetic responses for various progeny and parent selection methods. Attention is restricted to the state of steady genetic gains.

Progeny Selection Model

Let j and k be subscripts denoting ages of female and male nucleus parents with ℓ and n the corresponding subscripts for base parents. Consider the selection of nucleus female replacements. Suppose a fraction p_{jkf} of them are from the progeny of sires k years old and dams j years old in the nucleus, with $p_{\ell nf}$ the corresponding proportions for progeny born in the base. Let μ_{jk} and $\mu_{\ell n}$ denote the mean breeding values in parental age subclasses and $i_{jkf}E$ and $i_{\ell nf}$ denote the corresponding genetic selection differentials, expressed in units of $h^2\sigma_p$, where h^2 is the heritability and σ_p the phenotypic standard deviation within a parental age subclass in the base. E is an efficiency factor

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used to allow for possibly more accurate selection in the nucleus. Then the mean breeding value of nucleus female replacements is given by

$$\sum_j \sum_k p_{jkf}(\mu_{jk} + E_{ijkf}) + \sum_\ell \sum_n p_{\ell nf}(\mu_{\ell n} + i_{\ell nf})$$

The mean breeding value of male nucleus replacements is given by a similar expression with m replacing f as a subscript. Thus if μ_{ON} and μ_{OB} are the genetic means of all new-born nucleus and base progeny, while μ'_{ON} and μ'_{OB} are the genetic means of selected replacements, it follows that

$$\mu'_{ON} = \tfrac{1}{2} \sum_{b=f}^{m} \left(\sum_j \sum_k p_{jkb}\,(\mu_{jk} + E_{ijkb}) + \right.$$
$$\left. + \sum_\ell \sum_n p_{\ell nb}\,(\mu_{\ell n} + i_{\ell nf}) \right)$$

The summation over b indicates averaging over both sexes. Now by definition

$$\mu_{jk} = \tfrac{1}{2}(\mu'_j + \mu'_k) = \mu'_{ON} - \tfrac{1}{2}G(j + k)$$
$$\mu_{\ell n} = \tfrac{1}{2}(\mu'_\ell + \mu'_n) = \mu'_{OB} - \tfrac{1}{2}G(\ell + n)$$

and

$$\mu'_{OB} = \mu'_{ON} - (A + I_N - I_B)$$

where I_N and I_B are the overall selection differentials applied in selecting nucleus and base replacements, so that $A + I_N - I_B$ is the genetic difference between progeny of nucleus and base parents of the same age. It is shown later that $I_N - I_B = G(\Delta L)$ where ΔL is the difference in average age of parents in nucleus and base. Substituting these relations in the equation for μ'_{ON} and rearranging, we get

$$G = \frac{GN - X(A + G(\Delta L))}{LN}$$

where

CN is the mean selection differential within subgroups,

LN is the average age of parents at the birth of their progeny selected as nucleus replacements

and X is the proportional contribution of base-born individuals to nucleus replacements averaged over the two sexes.

Consideration of the selection of base replacements leads by a similar argument to

$$G = \frac{CB + Y(A + G(\Delta L))}{LB}$$

where Y is the proportional contribution of nucleus-born individuals to base replacements and CB and LB are the equivalents of CN and LN for base replacements.

These equations can be solved for G and A to give

$$G = \frac{X.CB + Y.CN}{X.LB + Y.LN}$$

and

$$A = \frac{CN.LB - CB.LN}{X.LB + Y.LN} - G\Delta L$$

Thus G can be regarded as a weighted sum of within-group selection differentials divided by a weighted sum of ages of parents of replacements. By dividing numerator and denominator of the first term of A by LN.LB, it is evident that A is the difference in selection efficiency in the two layers divided by a weighted mean of transfer rates.

Alternatively, we may use the principle of James (1977a) to state that the rate of genetic response equals the total selection differential divided by the time period over which the total selection differential is achieved. Defining the average age of parents of all nucleus and base progeny by ℓ_N and ℓ_B, we therefore have

$$G = \frac{I_N}{\ell_N} = \frac{I_B}{\ell_B} \text{ from which } I_N - I_B = G\Delta L$$

Now I_N can be partitioned into its three components by

$$I_N = CN + \Big((1-X)\ell_N + X\ell_B - LN\Big)G - XA$$

The first term is the within parental age subgroup selection differential, the second term arises from differential selection of replacements between parental age subgroups and the third term, -XA, is the selection differential due to differences between layers. Similarly,

$$I_B = CB + \Big(Y\ell_N + (1-Y)\ell_B - LB\Big) + YA.$$

James (1977b) grouped the within and between subgroup components into one and thus obtained his equations (13) and (14). Alternatively, rearranging our above expression for I_N we have

$$I_N = CN + G\Big(\ell_N - LN - X\Delta L\Big) - XA$$
$$G\ell_N = CN + G(\ell_N - LN) - X(A + G\Delta L)$$

and so

$$G = \frac{CN - X(A + G\Delta L)}{LN}$$

which is our earlier result. This demonstrates the equivalence of these results with those of James (1977b). The present form, however, has proved more convenient for calculation.

For the purpose of calculation, explicit expressions for the terms in the equations are required. Suppose a fraction α of all breeding females are used in the nucleus, the remaining $(1-\alpha)$ being used in the base. Let F be the number of progeny surviving to first mating per female mated. We assume no differences in fertility between age groups, or layers in both sexes. The proportion of all progeny born in the nucleus is, therefore, also α. The mating ratio

M, the number of females mated to each male, is assumed to be the same in nucleus and base.

Let S_j be the proportion of animals surviving from first mating to mating at age j years. Then, of all breeding females in the population, the fraction which are j years old nucleus females is $\alpha S_j/\sum_j S_j$, where the summation is over all ages of females used for breeding in the nucleus. Defining the total number of breeding females arbitrarily as one, there are F/2 female progeny from which $\alpha/\Sigma S_j$ must be selected as nucleus replacements. This implies an average proportion of progeny selected as nucleus female replacements of $2\alpha/F\sum_j S_j$, which is denoted by $\bar{P}_f$. Similarly, the average proportion selected for nucleus male replacements is $\bar{P}_m = 2\alpha/MF\sum_k S_k$, while those for base replacements are $\bar{Q}_f = 2(1\text{-}\alpha)/F\sum_\ell S_\ell$ and $\bar{Q}_m = 2(1\text{-}\alpha)/MF\sum_n S_n$.

Let P_{jkm}, $P_{\ell nm}$ be the proportions selected among nucleus male replacements from nucleus and base parental age subclasses of progeny. Replacing m subscripts by f gives those for nucleus female replacements while Q_{jkm}, *etc.*, are those for base replacements. We then have

$$\bar{P}_m = \frac{\alpha\sum_j\sum_k S_j S_k P_{jkm}}{\sum_j\sum_k S_j S_k} + \frac{(1-\alpha)\sum_\ell\sum_n S_\ell S_n P_{\ell nm}}{\sum_\ell\sum_n S_\ell S_n}$$

with similar expressions for $\bar{P}_f$, $\bar{Q}_m$ and $\bar{Q}_f$. These can be equated with previous expressions in order to ensure that the weighted sum of individual proportions selected is correct.

We can now define the terms in the equations using these parameters.

X = the relative contribution of base progeny to nucleus replacements

$$= \frac{(1-\alpha)\sum_\ell\sum_n S_\ell S_n P_{\ell nm}}{\bar{P}_m\sum_\ell\sum_n S_\ell S_n} + \frac{(1-\alpha)\sum_\ell\sum_n S_\ell S_n P_{\ell nf}}{\bar{P}_f\sum_\ell\sum_n S_\ell S_n}$$

Y = the relative contribution of nucleus progeny to base replacements

$$= \frac{\alpha\sum_j\sum_k S_j S_k Q_{jkm}}{\bar{Q}_m\sum_j\sum_k S_j S_k} + \frac{\alpha\sum_j\sum_k S_j S_k Q_{jkf}}{\bar{Q}_f\sum_j\sum_k S_j S_k}$$

CN = (CNM + CNF) / 2

where, for example

$$\mathrm{CNF} = \frac{\alpha\sum_j\sum_k S_j S_k P_{jkf} i_{jkf} E}{\bar{P}_f\sum_j\sum_k S_j S_k} + \frac{(1-\alpha)\sum_\ell\sum_n S_\ell S_n P_{\ell nf} i_{\ell nf}}{\bar{P}_f\sum_\ell\sum_n S_\ell S_n}$$

= the weighted mean of the within group selection differentials among females selected for the nucleus. CNM, CBM and CBF can be defined in a similar way.

LN = (LNF + LNM) / 2

where, for example

$$\mathrm{LNF} = \frac{\alpha\sum_j\sum_k S_j S_k P_{jkf}\,\frac{(j+k)}{2}}{\bar{P}_f\sum_j\sum_k S_j S_k} + \frac{(1-\alpha)\sum_\ell\sum_n S_\ell S_n P_{\ell nf}\,\frac{(\ell+n)}{2}}{\bar{P}_f\sum_\ell\sum_n S_\ell S_n}$$

Parent selection Model

In this case, expressions for G and A are derived by equating the genetic mean of the current unselected progeny crop to the mean breeding value of their selected parents. Let p_j be the proportional genetic contribution of j year old nucleus-born breeding females to progeny born in the nucleus, while p_ℓ is the corresponding proportion from base-born females. p_k and p_n are the corresponding proportions for males. Then μ_{ON}, the newborn nucleus mean is given by

$$\mu_{ON} = \tfrac{1}{2}\Big(\sum_j p_j(\mu_j + i_j E) + \sum_\ell p_\ell(\mu_\ell + i_\ell) + \sum_k p_k(\mu_k + i_k E) + \sum_n p_n(\mu_n + i_n)\Big)$$

Since $\mu_j = \mu_{ON} - jG$ and $\mu_\ell = \mu_{ON} - \ell G - A$ and so on, μ_{ON} can be eliminated to give

$$G = \frac{CN - A.X}{\ell_n}$$

Similarly, after starting with the equivalent equation for the mean of base progeny, we get

$$G = \frac{CB + A.Y}{\ell_B}$$

and from these equations we obtain

$$G = \frac{CN.Y + CB.X}{\ell_N Y + \ell_B X}$$

and

$$A = \frac{CN.\ell_B - CB.\ell_N}{X.\ell_B - Y.\ell_N},$$

again in agreement with James (1977b). The chief difference in the form of these equations and those for progeny selection is the absence of GΔL in the expression for A in parent selection and the use of ℓ_N and ℓ_B rather than LN and LB. The exact definitions of terms also differ, as we now show.

Because there are αF/2 nucleus progeny and (1-α)F/2 base progeny of each sex reaching mating age annually, then there are $\tfrac{1}{2}F(\alpha\sum_j S_j + (1\text{-}\alpha)\sum_\ell S_\ell)$ female yearlings available from which breeding females may be selected. Thus, with parent selection, the greater the number of age groups the larger the number available for selection, whereas in progeny selection the same number are available for selection irrespective of the number of age groups. On the other hand, in parent selection the same number must be selected no matter how many age groups are present, while in progeny selection the more age groups, the fewer replacements need to be selected.

Let P_j and P_ℓ be the fractions selected as nucleus female replacements from j year-old nucleus-born and ℓ year-old base-born females. Then the number of nucleus females selected is $\frac{1}{2}F(\alpha\Sigma S_jP_j + (1\text{-}\alpha)\sum_\ell S_\ell P_\ell)$. But by our earlier definition this is also α, so that

$$\alpha\sum_j S_jP_j + (1\text{-}\alpha)\sum_\ell S_\ell P_\ell = 2\alpha/F.$$

Clearly there are corresponding equations for nucleus males, base males and base females.

The terms in the expressions for G and A can now be defined explicitly. Thus

X = the proportional contribution of base-born individuals to the nucleus gene pool

$$= \frac{\frac{1}{2}(1\text{-}\alpha)\sum_\ell P_\ell S_\ell}{\alpha\sum_j P_jS_j + (1\text{-}\alpha)\sum_\ell P_\ell S_\ell} + \frac{\frac{1}{2}(1\text{-}\alpha)\sum_n P_nS_n}{\alpha\sum_k P_kS_k + (1\text{-}\alpha)\sum_n P_nS_n}$$

Y = the proportional contribution of nucleus-born individuals to the base gene pool

$$= \frac{\frac{1}{2}\alpha\sum_j Q_jS_j}{\alpha\sum_j Q_jS_j + (1\text{-}\alpha)\sum_\ell Q_\ell S_\ell} + \frac{\frac{1}{2}\alpha\sum_k Q_kS_k}{\alpha\sum_k Q_kS_k + (1\text{-}\alpha)\sum_n Q_nS_n}$$

CN = (CNM + CNF) / 2

where

CNF = the within age group selection differential for females for the nucleus

$$= \frac{\alpha\sum_j S_jP_ji_jE \quad + \quad (1\text{-}\alpha)\sum_\ell S_\ell P_\ell i_\ell}{\alpha\sum_j P_jS_j \quad + \quad (1\text{-}\alpha)\sum_\ell P_\ell S_\ell}$$

CNM and CB (={CBM + CBF} / 2) are defined in a similar way.

ℓ_N = $\frac{1}{2}(\ell_{Nm} + \ell_{Nf})$ where

$$\ell_{Nf} = \frac{\alpha\sum_j S_jP_jj \quad + \quad (1\text{-}\alpha)\sum_\ell S_\ell P_\ell \ell}{\alpha\sum_j S_jP_j \quad + \quad (1\text{-}\alpha)\sum_\ell S_\ell P_\ell \ell}$$

Under parent selection therefore G is the ratio of the overall mean within age group selection differential to the average age of (selected) parents.

Criteria for Optimising Transfer Rates between Layers

In broad principle the criterion for choosing transfer rates so as to maximise the selection differentials I_N and I_B, and hence G, is that the expected breeding value of all truncation points should be the same. Bichard *et al* (1973) and Hopkins and James (1977) have discussed the application of this principle to single layer breeding programmes. In practice, however, how one should apply this principle to nucleus breeding schemes where different selection strategies are used in the nucleus and base is not immediately obvious. Complications may arise in other situations too as will be shown later for the case where phenotypic selection is practised in both layers.

In this study expressions for optimum relationships between truncation points were derived for nine combinations of nucleus and base selection strategies. These combinations are defined in Appendix I along with detailed results for each.

The general procedure for optimizing transfer rates comprises the following four steps.

Step 1. Define an expression for the genetic mean of those selected (or of the selection differential).

Step 2. Add a Lagrange multiplier based on the constancy of average proportions or total numbers selected.

Step 3. Partially differentiate the resulting expression with respect to each nucleus proportion, sum the resulting expressions over all nucleus groups and equate this sum to zero. Repeat this procedure differentiating with respect to each base proportion to obtain a second general equation.

Step 4. Solve to obtain a general relationship between truncation points used in nucleus and base. These define the general criteria for optimizing transfer rates. For instance, provided that, *a priori*, the only relationship between the selection proportions is that their weighted sum is a constant, the general equation relating nucleus to base truncation points in the selection of female progeny under progeny selection is

$$\frac{\sum_\ell\sum_n S_\ell S_n(\mu_\ell + X_{\ell nf})}{\sum_\ell\sum_n S_\ell S_n} = \frac{\sum_j\sum_k S_jS_k(\mu_{jk} + X_{jkf})}{\sum_j\sum_k S_jS_k} \tag{1}$$

or, alternatively

$$\frac{\sum_\ell\sum_n S_\ell S_nX_{\ell nf}}{\sum_\ell\sum_n S_\ell S_n} = \frac{\sum_j\sum_k S_jS_kX_{jkf}}{\sum_j\sum_k S_jS_k} + A \tag{2}$$

where X is the truncation point deviation from μ.

Under parent selection the general equation for selection among females is

$$\frac{\sum_\ell S_\ell(\mu_\ell + X_\ell)}{\sum_\ell S_\ell} = \frac{\sum_j s_j(\mu_j + X_jE)}{\sum_j S_j} \tag{3}$$

or, alternatively,

$$\frac{\sum_{\ell} S_{\ell}(X_{\ell} - \ell G)}{\sum_{\ell} S_{\ell}} = \frac{\sum_{k} S_k (X_k E - kG)}{\sum_{k} S_k} + A \qquad (4)$$

Equations 1 and 3 are applicable to both steady-state and non-steady-state situations and indicate that the weighted mean of *expected* breeding values at truncation points should be the same in both layers. Equations 2 and 4 come from making a simple rearrangement in either case and can be more useful in the steady-state situation. As shown in Appendix I, these equations are easily adapted to specific strategy combinations.

Discussion

Apart from basic differences between parent and progeny selection systems in the single layer situation (see Hopkins and James, 1977) there are further basic differences in the two layer or nucleus breeding situation, some of which have already been described. These differences are now summarised.

The first difference concerns the difference between the mean of the nucleus and base populations under selection. Under progeny selection this difference has been defined as A. Under parent selection the difference is $A + G(\sum_{\ell} \ell S_{\ell}/\sum_{\ell} S_{\ell} - \sum_{j} j S_j/\sum_{j} S_j)$ for females and $A + G(\sum_{n} n S_n/\sum_{n} S_n - \sum_{k} k S_k/\sum_{k} S_k)$ for males. This implies that where the number of base age groups exceeds the number of nucleus age groups the difference between layers would be greater under parent selection, thus increasing the between-layer variance. In fact the larger A values under progeny selection can offset this effect almost completely.

The second basic difference is that, under parent selection, selections are from two different sets of distributions for males and females but from only one set in progeny selection. Thus, where nucleus and base age structures differ, truncation point differences (*i.e.*, transfer rates) can be optimised within each sex under parent selection while truncation point differences are, in general, the same for both sexes under progeny selection. In this sense parent selection has an extra 'degree of freedom'.

Third, there are differences in concept of age structure. In progeny selection 'the age of parents' and 'number of age groups' is based on where the parents are used irrespective of their origins. In parent selection 'the number of age groups' is based on place of birth and use of parents. Further, under progeny selection, the 'number of age groups' refers to the number of equally (except for deaths) represented age groups while under parent selection it refers to the number of age groups represented whether equally or unequally.

A fourth and related difference is the ability of parent selection systems in optimising transfer rates to allow for the use of parents in the nucleus followed by the use of the same individuals in the base. In fact, there are three categories of parent selection systems. In the first category are systems which assume that once an individual is selected for the nucleus or base it remains there until culled for age. In the second category are systems where the initial performance of the individual determines (a), whether or not it should be selected at the outset for the nucleus or for the base, (b), how many years it should remain in the layer in which it is first used and (c), if it was first used in the nucleus, whether it should then be used in the base and, if so, for how long. In the third category are systems where selection among nucleus born individuals is based on the mean of records accumulated over their lifetime according to procedures outlined by Hopkins and James (1977). This strategy assumes that all nucleus-born animals are retained and assessed annually whether they are chosen for the replacements-producing breeding population or not. Each year estimates of their breeding value are updated to include the effect of the last measure of performance. The estimated breeding value of a nucleus-born individual may therefore fluctuate so that, in addition to the possibilities already described, there are the additional possibilities of nucleus-born animals, which have been relegated to the base or eliminated from the replacement-producing population altogether, being reinstated in the nucleus or base depending on their performane in the interim.

Throughout this paper the symbol ℓ_N (ℓ_B) has been used to describe the average age of parents used in the nucleus (base) while LN (LB) has described the average age of parents of replacements (progeny selection) and the average age of replacements (parent selection). Alternatively, it would have been possible and, in a sense more consistent, to define LN (LB) as the average age of parents of selected individuals in progeny selection or parents used in parent selection, the ages in each case corresponding to the within-group selection differential (*i.e.*, average age *after* selection). Correspondingly, it would have been possible to define ℓ_N (ℓ_B) as the average age pertaining to the situation before selection in the parent selection systems as well as in the progeny systems. Similarly, one could redefine A to be the average difference between the nucleus and base groups under selection in parent selection as well as progeny selection. With these changes of definition equations defining A and G under progeny selection are directly applicable to parent selection systems.

Although it has been assumed in both models that F is the same in all age groups, both sexes and both layers, this assumption can be relaxed as shown in Appendix II. The assumption that the time unit is years can also be relaxed by substituting 'time period' for 'years' throughout the text. Pig breeders, for instance, would probably use a 'half year' rather than 'year' as the basic time unit.

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Appendix I

Relationships between Truncation Points used to Optimise Transfer Rates between Layers for Nine Strategy Combinations

The following parent and progeny selection strategies were used

Progeny selection:

- optimal use of genetic differences between parental age subclasses (PG)
- phenotypic selection, *i.e.*, some use of genetic differences between parental age subgroups (PH)
- selection of the same proportions from each parental age subclass, *i.e.*, no use of genetic differences between parental age subclasses (EQPG)

Parent selection:

- optimal use of genetic differences between age groups. All selection decisions are based on a single record taken before first mating (PR)
- the same strategy but selection decisions are based on all records accumulated over the individual's lifetime up to the time of selection (AR). Details of this strategy are given by Hopkins and James (1977)
- selection of the same proportions from each age group (EQPR)

In all parent selection strategies it is assumed that EQPG selection is practiced within each age group.

Selection procedures in nucleus breeding schemes can be described by a combination of these selection strategies. For example, PR/EQPR implies that PR selection is employed in selection among nucleus-born animals and EQPR selection among those which are base-born.

Below, optimum truncation point relationships for nine combinations of systems are given and the first eight of these are derived from adaptation of equations 2 and 4 in the text. Throughout, all truncation points are related to the first truncation point in the nucleus.

EQPG/EQPG

Here $X_{\ell nf}$ and X_{jkf} are constants (X_B and X_N respectively) so that equation 1 becomes

$$X_B = X_N E + A.$$

EQPR/EQPR

From equation 4

$$\text{Females} \quad X_B = X_N E + A - G\left(\frac{\sum_j jS_j}{\sum_j S_j} - \frac{\sum_\ell \ell S_\ell}{\sum_\ell S_\ell}\right)$$

$$\text{Males} \quad X_B = X_N E + A - G\left(\frac{\sum_k kS_k}{\sum_k S_k} - \frac{\sum_n nS_n}{\sum_n S_n}\right)$$

The last term in each of these equations is an adjustment for the effect of differences in number of age groups of that sex in the nucleus and base on the overall means of nucleus and base distrubtions describing the population under selection. Note that $X_B - X_N E$ in these equations defines the average genetic difference between the means of these two series of distributions. The equations also show that, while EQPG = EQPR in the single layer situation, EQPR/EQPR selection, is superior to EQPG/EQPG selection because truncation points are optimised for each sex. (See Discussion.)

PG/EQPG

Nucleus $X_{jk} = X_{22N} + ½G(j + k-4) / E$

Base $X_B = X_{22N}E + A + ½G\left(\frac{\sum_j\sum_k S_jS_k(j+k-4)}{\sum_j\sum_k S_jS_k}\right)$

PG/PG

Nucleus $X_{jk} = X_{22N} + ½G(j+k-4) / E$

Here $\mu'_{\ell n} + X_{\ell nf} = \mu'_{jk} + X_{jkf}E = \text{constant}$, *i.e.*,

$X_{\ell n} = X_{22N}E + A + G\Delta L + ½G(\ell + n-4)$

PR/EQPR

Nucleus $X_j = X_{2N} + G(j-2) / E.$

Base $X_\ell = X_{2N}E + A + G \frac{\sum_\ell S_\ell(\ell-2)}{\sum_\ell S_\ell}$

AR/EQPR

Nucleus $X_j = \{X_{2N} + G(j-2)/E\}\sqrt{\{1 + (j-2)r\}/(j-1)}$

Base $X_\ell = X_{2N}E + A + G \frac{\sum_\ell S_\ell(\ell-2)}{\sum_\ell S_\ell}$

PR/PR

Nucleus $X_j = X_{2N} + G(j-2) / E$

Here $\mu_\ell + X_\ell = \mu_j + X_j E$, *i.e.*,

$$X_\ell = X_{2N}E + A + G(\ell - 2)$$

AR/PR

Nucleus $X_j = \{X_{2N} + G(j-2)/E\}\sqrt{\{1 + (j-2)r\}/(j-1)}$

Base $X_\ell = X_{2N}E + A + G(\ell - 2)$

The general relationships given above hold where, *a priori*, the only relationship between the selection proportions is absorbed within the Lagrange multiplier. This is not the case for the PH/PH combination for which optimum truncation points are given by

Nucleus $X_{\ell k} = X_{22N} + \tfrac{1}{4}Gh^2(j+k-4)/2E$

Base $X_{\ell n} = X_{22N}E + A + G\Delta L + \text{DIFZ}$

where

$$\text{DIFZ} = \tfrac{1}{2}G\left(\frac{(1-h^2)\sum\limits_{\ell}\sum\limits_{n} S_\ell S_n Z_{\ell n}(\ell + n)}{\sum\limits_{\ell}\sum\limits_{n} S_\ell S_n Z_{\ell n}} - \frac{(1-h^2E^2)\sum\limits_{j}\sum\limits_{k} S_j S_k Z_{jk}(j+k)}{\sum\limits_{j}\sum\limits_{k} S_j S_k Z_{jk}}\right)$$

We can offer no intuitive explanation for this last term. A similar situation exists for 'phenotypic' selection under parent selection.

Appendix II

Accomodation of Differential Fertility Rates

Progeny selection

Let $F_N(F_B)$ be the average female fertility rate in the nucleus (base) so that $M_N F_N(M_B F_B)$ describes the average male fertility in nucleus (base). Thus, by definition,

$$F_N = \Sigma F_j S_j / \Sigma S_j, \qquad F_B = \Sigma F_\ell S_\ell / \Sigma S_\ell$$

$$M_N F_N = \Sigma F_k S_k / \Sigma S_k, \quad M_B F_B = \Sigma F_N S_n / \Sigma S_n$$

where M_N and M_B are the mating ratios used in nucleus and base and the F_j, *etc.*, are the fertility rates within an age-sex group.

The number of nucleus-born (base-born) progeny of each sex reared to mating is $\tfrac{1}{2}\alpha F_N$ $(\tfrac{1}{2}(1-\alpha)F_B)$ so that the total number of progeny of each sex available for selection as one-year olds is $\tfrac{1}{2}(\alpha F_N + (1-\alpha)F_B)$. Of the α nucleus females $1/\Sigma S_j$ are required for replacements. Thus we have two expressions for $\overline{P}_f$, the seond one being given by definition:

$$\overline{P}_f = \frac{\alpha / \Sigma S_j}{\tfrac{1}{2}(\alpha F_N + (1-\alpha)F_B)}$$

$$= \frac{\alpha F_N\left(\dfrac{\Sigma\Sigma S_j S_k F_j F_k P_{jkf}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B\left(\dfrac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nf}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right)}{\alpha F_N + (1-\alpha)F_B}$$

Therefore

$$\alpha F_N\left(\frac{\Sigma\Sigma S_j S_k F_j F_k P_{jkf}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B \left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nf}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right) = \frac{2\alpha}{\Sigma S_j}$$

Similarly, from the corresponding expression for $\overline{Q}_f$ we get

$$\alpha F_N\left(\frac{\Sigma\Sigma S_j S_k F_j F_k Q_{jkf}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B \left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nf}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right) = \frac{2(1-\alpha)}{\Sigma S_\ell}\ .$$

Now for selection of male replacements for the nucleus we have

$$\overline{P}_m = \frac{\alpha / M_N \Sigma S_k}{\tfrac{1}{2}(\alpha F_N + (1-\alpha)F_B)} = \alpha F_N\left(\frac{\Sigma\Sigma S_j S_k F_j F_k P_{jkm}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B\left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nm}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right)$$

so that

$$\alpha F_N\left(\frac{\Sigma\Sigma S_j S_k F_j F_k P_{jkm}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B \left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nm}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right) = \frac{2\alpha}{M_N \Sigma S_k}\ .$$

Similarly, from the corresponding equation for $\overline{Q}_m$ we get

$$\alpha F_N\left(\frac{\Sigma\Sigma S_j S_k F_j F_k Q_{jkm}}{\Sigma\Sigma S_j S_k F_j F_k}\right) + (1-\alpha)F_B \left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n Q_{\ell nm}}{\Sigma\Sigma S_\ell S_n F_\ell F_n}\right).$$

$$X = \frac{(1-\alpha)F_B}{\alpha F_N + (1-\alpha)F_B}\left(\frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nf}}{\overline{P}_f \Sigma\Sigma S_\ell S_n F_\ell F_n} + \frac{\Sigma\Sigma S_\ell S_n F_\ell F_n P_{\ell nm}}{\overline{P}_m \Sigma\Sigma S_\ell S_n F_\ell F_n}\right)$$

$$Y = \frac{\alpha F_N}{\alpha F_N + (1-\alpha)F_B}$$

$$\left(\frac{\Sigma\Sigma S_jS_kF_jF_kP_{jkf}}{\overline{P}_f\Sigma\Sigma S_jS_kF_jF_k} + \frac{\Sigma\Sigma S_jS_kF_jF_kP_{jkm}}{\overline{P}_m\Sigma\Sigma S_jS_kF_jF_k}\right)$$

$$\mathrm{CNF} = \frac{1}{\overline{P}_f(\alpha F_N + (1\text{-}\alpha)F_B)}\left(\alpha F_N \frac{\Sigma\Sigma S_jS_kF_jF_kP_{jkf}i_{jkf}E}{\Sigma\Sigma S_jS_kF_jF_k}\right.$$

$$\left. + (1\text{-}\alpha)F_B \frac{\Sigma\Sigma S_\ell S_nF_\ell F_nP_{\ell nf}i_{\ell nf}}{\Sigma\Sigma S_\ell S_nF_\ell F_n}\right)$$

CNM is defined by substituting the m subscript for f.

CBF and CBM are defined by substituting Q for P in their corresponding equations for the nucleus.

LNM, LNF, LBM and LBF are defined by substituting ½(j + k) or ½(ℓ + n) for i and omitting E.

Parent Selection

In this case F_N and F_B are defined by

$$F_N = \frac{\Sigma S_jF_jP_j}{\Sigma S_jF_j}, \qquad F_B = \frac{\Sigma S_\ell F_\ell P_\ell}{\Sigma S_\ell F_\ell}$$

and there are $\frac{1}{2}(\alpha F_N\ \Sigma S_j + (1\text{-}\alpha)\ F_B\ \Sigma S_\ell)$ female candidates for selection out of which α are selected for the nucleus. Thus

$$\overline{P}_f = \frac{2\alpha}{\alpha F_N\Sigma S_j + (1\text{-}\alpha)F_B\Sigma S_\ell}$$

$$= \frac{\frac{1}{2}(\alpha F_N\Sigma S_jP_j + (1\text{-}\alpha)F_B\Sigma S_\ell P_\ell)}{\frac{1}{2}(\alpha F_N\Sigma S_j + (1\text{-}\alpha)F_B\Sigma S_\ell)}$$

That is

$$\alpha F_N\Sigma S_jP_j + (1\text{-}\alpha)F_B\Sigma S_\ell P_\ell = 2\alpha.$$

From the corresponding expression for $\overline{Q}_f$ we get

$$\alpha F_N\Sigma S_jQ_j + (1\text{-}\alpha)F_B\Sigma S_\ell Q_\ell = 2(1\text{-}\alpha)$$

In males we wish to select α/M_N nucleus replacements out of $\frac{1}{2}(\alpha F_N\Sigma S_kP_k + (1\text{-}\alpha)F_B\Sigma S_nP_n)$ so that

$$\overline{P}_m = \frac{2\alpha/M_N}{\alpha F_N\Sigma S_k + (1\text{-}\alpha)F_B\Sigma S_n}$$

$$= \frac{\frac{1}{2}\{\alpha F_N\Sigma S_kP_k + (1\text{-}\alpha)F_B\Sigma S_nP_n\}}{\frac{1}{2}\{\alpha F_N\Sigma S_k + (1\text{-}\alpha)F_B\Sigma S_n\}}$$

which leads to

$$\alpha F_N\Sigma S_kP_k + (1\text{-}\alpha)F_B\Sigma S_nP_n = 2\alpha/M_N$$

and from the expression for $\overline{P}_f$ we get

$$\alpha F_N\Sigma S_jP_j + (1\text{-}\alpha)F_B\Sigma S_\ell P_\ell = 2\alpha$$

Similarly,

$$\alpha F_N\Sigma S_kQ_k + (1\text{-}\alpha)F_B\Sigma S_nQ_n = 2(1\text{-}\alpha)/M_B$$

and

$$\alpha F_N\Sigma S_jQ_j + (1\text{-}\alpha)F_B\Sigma S_\ell Q_\ell = 2(1\text{-}\alpha)$$

$$X = \frac{(1\text{-}\alpha)F_B\Sigma S_\ell P_\ell}{\alpha F_N\Sigma S_j + (1\text{-}\alpha)F_B\Sigma S_\ell} + \frac{(1\text{-}\alpha)F_B\Sigma S_nP_n}{\alpha F_N\Sigma S_k + (1\text{-}\alpha)F_B\Sigma S_n}$$

$$Y = \frac{\alpha F_N\Sigma S_jP_j}{\alpha F_N\Sigma S_j + (1\text{-}\alpha)F_B\Sigma S_\ell} + \frac{\alpha F_N\Sigma S_kP_k}{\alpha F_N\Sigma S_k + (1\text{-}\alpha)F_B\Sigma S_n}$$

$$\mathrm{CNF} = \frac{\alpha F_N\Sigma S_jP_j i_jE \quad + \quad (1\text{-}\alpha)F_B\Sigma S_\ell P_\ell i_\ell}{\alpha F_N\Sigma P_jS_j \qquad (1\text{-}\alpha)F_B\Sigma P_\ell S_\ell}$$

Expressions for all other components of the within group selection differentials and generation intervals follow the same pattern. All that is required is to insert F_N and F_B at appropriate points in numerator and denominator.

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