

# DEVELOPMENTS IN OPEN NUCLEUS BREEDING SYSTEMS\*

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## SUMMARY

Recent developments in the theory of open nucleus breeding systems are reviewed and illustrated by an example of an Australian Merino system. Equations are given for multi-flock systems. Emphasis is given to the importance of improved accuracy of selection of males in the nucleus, and it is shown that two-stage selection of base females may give useful gains. Progeny testing is shown to be useful when progeny information significantly improves estimation of overall breeding value. However, benefits of other changes introduced together with progeny testing should not be attributed to it. Rates of inbreeding may actually be reduced in progeny testing programs because of the longer generation interval. An example shows that differences in breeding objective may determine whether or not progeny testing should be adopted.

## INTRODUCTION

Open nucleus systems are hierarchical breeding systems in which animals may be transferred between levels in both directions. The simplest open nucleus system has two mating groups; a nucleus of elite animals, and a base in which the general flock is mated. In general, there may be more than two levels, and there may be several flocks in the one level. A typical group breeding scheme consists of a nucleus and 10 to 15 contributing base flocks. The Australian Merino Society scheme has three levels; a central nucleus, 122 ram breeding cooperatives, and more than 1000 contributors. The properties of such assortative mating structures were reviewed by James (1982). Due to increased additive genetic variation due to between level differences, expected genetic gain in open nucleus systems is more rapid than in equivalent single flocks, provided more females than males need to be replaced. The greater selection differential on the dams of sires path in open nucleus systems more than compensates for the reduced differential on the sires of dams path.

Often the base is managed for commercial production and the nucleus to breed superior sires. Hopkins (1978) emphasized that using more efficient selection strategies and short generation lengths in the nucleus would increase rates of gain. More recently, further methods of improving genetic gains in open nucleus systems have been explored. These include using more accurate selection indices and selecting in two stages on different indices (Mueller, 1984), using family information in selection indices (Mueller *et al.*, 1984), in particular progeny testing (Mueller and James, 1984). This paper will review the relevant theory and discuss applications to sheep breeding programs.

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\* INTA Bariloche, Comunicación Técnica PA Nro. 175. Trabajo presentado al Segundo Congreso Mundial de Ovinos y Bovinos de Carne, Pretoria, Sudáfrica, 16-19 abril de 1984 y publicado en los correspondientes Proceedings (Editores J Hofmeyer y E Meyer), pag 204-213.

## PREDICTION OF GENETIC GAIN AND LAG

### Systems with a single base flock

Equations to predict asymptotic genetic gain and lag in a system with a single base were given by James (1977). If  $w$  and  $y$  are the proportions of base sires and dams born in the nucleus, and  $v$  and  $x$  are the proportions of nucleus sires and dams born in the base, the genetic selection differentials for the nucleus ( $C_N$ ) and base ( $C_B$ ) are given by:

$$C_N = ((1 - v) D_{NMN} + v D_{BMN} + (1 - x) D_{NFN} + x D_{BFN}) / 2 \quad (1a)$$

$$C_B = ((1 - w) D_{BMB} + w D_{NMB} + (1 - y) D_{BFB} + y D_{NFB}) / 2 \quad (1b)$$

$D_{NMN}$  is the genetic selection differential of nucleus born males used in the nucleus,  $D_{BFN}$  is the genetic selection differential for base born females used in the nucleus, etc. Let  $g$  be the proportion of all transfers originating in the nucleus, so that  $g = (w+y) / (w+y+v+x)$ , and let  $l_N$  and  $l_B$  be the generation intervals in nucleus and base. Then the steady state rate of genetic gain in nucleus and base is given by:

$$G = (g C_N + (1 - g) C_B) / (g l_N + (1 - g) l_B), \quad (2)$$

and the lag, or difference in genetic mean between nucleus and base is given by

$$A = 2 (l_B G - C_B) / (w + y). \quad (3)$$

The lag is often expressed in terms of years of improvement,  $L = A / G$ .

### Group breeding schemes

The previous equations can be adapted to group breeding schemes, where each flock may differ in selection accuracy, generation length, etc. If the parameters for the  $i$  th flock are denoted by an  $i$  subscript, and  $\sum$  denotes summation over all flocks, the genetic selection differential and generation length for the nucleus are

$$C_N = [(1 - \sum v_i) D_{NMN} + \sum v_i D_{BMNi} + (1 - \sum x_i) D_{NFN} + \sum x_i D_{BFNi}] / 2 \quad (4a)$$

$$l_N = [(1 - \sum v_i) l_{NMN} + \sum v_i l_{BMNi} + (1 - \sum x_i) l_{NFN} + \sum x_i l_{BFNi}] / 2 \quad (4b).$$

The corresponding values for the  $i$  th flock are:

$$C_{Bi} = [(1 - w_i) D_{BMBi} + w_i D_{NMBi} + (1 - y_i) D_{BFBi} + y_i D_{NFBi}] / 2 \quad (5a)$$

$$l_{Bi} = [(1 - w_i) l_{BMBi} + w_i l_{NMBi} + (1 - y_i) l_{BFBi} + y_i l_{NFBi}] / 2. \quad (5B)$$

The steady state rate of genetic gain in all flocks is then:

$$G = (C_N + \sum((1 - g_i) C_{Bi} / g_i)) / (l_N + \sum((1 - g_i) l_{Bi} / g_i)). \quad (6)$$

The genetic lag of the  $i$  th member flock behind the nucleus is:

$$A_i = 2 (l_{Bi} G - C_{Bi}) / (w_i + y_i) \quad (7)$$

or  $A_i / G$  years.

### Optimum transfer rates and nucleus size

The transfer rates and nucleus size which maximize rate of genetic gain  $G$ , can be found by trial and error, using the principle that truncation points of expected breeding values of contributing groups of individuals in nucleus and base should coincide (Hopkins and James, 1978). Assuming that all animals are selected on the same criterion, and generation interval is the same in nucleus and base, James (1977) found optimum designs for a range of conditions. The well known rules of thumb, namely 10% of the population in the nucleus, and half of the nucleus dam replacements transferred from the base, are close to optimum. With shorter generation interval and more efficient selection strategy in the nucleus, Hopkins (1978) showed that, due to increased lag, fewer base females qualify for the nucleus, but genetic gain is more rapid. Mueller (1984) investigated optimum designs when different selection indices were used to select sires and dams, in nucleus and base. General guidelines for the design of open nucleus systems were also given by Parker and Rae (1982).

Detailed optimization of group breeding schemes with many flocks is laborious because many truncation points must be equated simultaneously. If member flocks are similar in genetic mean, selection accuracy, and flock composition, as would usually be the case, all flocks could be treated as a single base without significant loss of accuracy. Any initial differences in genetic mean would be evened out after a few years. If member flocks differ greatly in selection accuracy or flock composition, upward transfer rates should be greater from the more efficient flocks. In such conditions gains and lags must be calculated from equations (6) and (7). Guy and Steane (1980) attempted such an analysis for a British cattle system with 4 members.

### A standard situation

The equations presented earlier are general, and allow for arbitrary gene flows. The following restricted situation will be common in practice. All sires are bred in the nucleus ( $w = 1, v = 0$ ). Half of the nucleus dams come from the base ( $x = 0.5$ ), but no nucleus females are transferred to the base ( $y = 0$ ). Then equations (2) and (3) simplify to:

$$G = (2 D_{NMN} + D_{NMB} + D_{BFN} + D_{BFB}) / (4 l_N + 2 l_B) \quad (8)$$

$$A = 2 l_B G - D_{NMB} - D_{BFB}. \quad (9)$$

## Example

To illustrate various points, we shall consider an open nucleus system for Australian Merino sheep. There are 4 dam age groups and 1 sire age group. Each ewe rears 0.8 progeny per year, lambing first at 2 years of age. Each sire is mated to 100 ewes, and 10% of the population is in the nucleus. Therefore, the standardised selection differentials needed to calculate the D-values in (8) are 2.338, 1.152, 1.133, 2.211 and 0.464. The program aims to improve breeding value H by selection on an index I. The standard deviation of breeding value is  $\sigma_H$ , and  $r_{HI}$  denotes the correlation between H and I. The genetic selection differentials are then  $r_{HI} \sigma_H$  times the standardised selection differentials.

Let H be the objective defined by Ponzoni (1979) expressed on a yearly basis:

$$H = 2.76 \text{ CFW} - 0.39 \text{ FD} + 14 \text{ NLW} + 0.24 \text{ WW} + 0.03 \text{ MBW},$$

where CFW = clean fleece weight, WW = weaning weight, FD = fiber diameter, MBW = mature body weight and NLW = number of lambs weaned.

Using parameters assumed by Ponzoni (1979), we find  $\sigma_H = 2.4737$  Australian dollars/ewe/year.

Suppose all replacements are selected on greasy fleece weight (GFW), whose correlation with H is 0.1592. Then, measuring gain in units of  $\sigma_H$ :

$$G = (2 \times 2.338 + 1.152 + 1.133 + 2.211 + 0.464) 0.1592 / (4 \times 2.75 + 2 \times 2.75) = 0.093,$$

and  $A = 0.254$ , or the base lags 2.73 years behind the nucleus.

## EFFECTS OF CHANGING SELECTION ACCURACY

### Improving selection accuracy in the nucleus

In the standard situation the nucleus contributes  $2/3$  of the genes for the total response, and since many more dams than sires must be selected for replacement, it is obvious that most effort should be spent on selection of sires. Improvement in the selection accuracy of sires is more than 3 times as effective as a similar improvement for nucleus females. By testing arbitrary index sets, Mueller (1984) showed that the relative improvement in response due to further measurements on males depend on relative accuracy's of indices used in nucleus and base. For instance, if rams are selected on an index combining clean fleece weight and yearling body weight, (YBW), the response is 25% to 45% greater than if they are selected on greasy fleece weight alone. The lower change corresponds to very accurate selection in the base.

In the example discussed above, suppose that for ram hoggets in the nucleus, fleece samples are taken for measurement of CFW and FD, and yearling body weights are also recorded at shearing time. Then rams can be selected on an index I combining CFW, FD, and YBW, whose correlation with H is 0.3686, and in units of  $\sigma_H$ :

$$G = ((2 \times 2.338 + 1.152) 0.3686 + (1.133 + 2.211 + 0.464) 0.1592) / 16.5 = 0.167.$$

The lag is 2.51 years. If, in addition, females in the nucleus are selected on I rather than GFW alone, the gain is 0.181 and the lag is 2.75 years.

### Improving selection accuracy in the base

The base flocks contribute a minor part of total response unless their selection procedures are very efficient. More accurate selection indices require more measurements on relevant traits. Costs might prevent a breeder measuring all his flock, but it might be possible to obtain a better index for at least some females. Selection could proceed in two stages, with a fraction  $q_1$  being selected on index  $I_1$ , and then a fraction  $q_{BFN}$  (the fraction of base born females required for the nucleus) out of the  $q_1$  being selected on a more accurate index  $I_2$ . Let  $q_{BFB} + q_{BFN} = q_{BFT}$ , the total proportion of females selected from the base, and let  $s(q)$  be the standardised selection differential when a fraction  $q$  is selected by truncating a standard normal distribution at the point  $t(q)$ . The genetic differentials involving base females become:

$$D_{BFN} = s(q_1) r_{HI1} + s(q_{BFN} / q_1) r_{HI2} \sqrt{(1 - r^2 c)}$$

$$D_{BFB} = (q_{BFT} s(q_{BFT}) r_{HI} - q_{BFN} D_{BFN}) / q_{BFB}.$$

The factor  $\sqrt{(1 - r^2 c)}$  accounts for the reduced variance in  $I_2$  after selection on  $I_1$ ,  $r$  is the correlation between  $I_1$  and  $I_2$  and  $c = s(q_1) (s(q_1) - t(q_1))$ . The equation for  $D_{BFB}$  is valid when all females scored for  $I_2$  are used for breeding. If  $q > q_{BFT}$  there would be extra gains due to increased  $D_{BFB}$ . However, such a case is of little practical interest.

In order to decide on the proportion of animals to be saved for further measurements, benefits from extra response must be balanced against costs of extra measurements. The breeder would like to take extra measurements on only a few animals, but still obtain a high proportion of the response attained when all animals are selected on  $I_2$ .

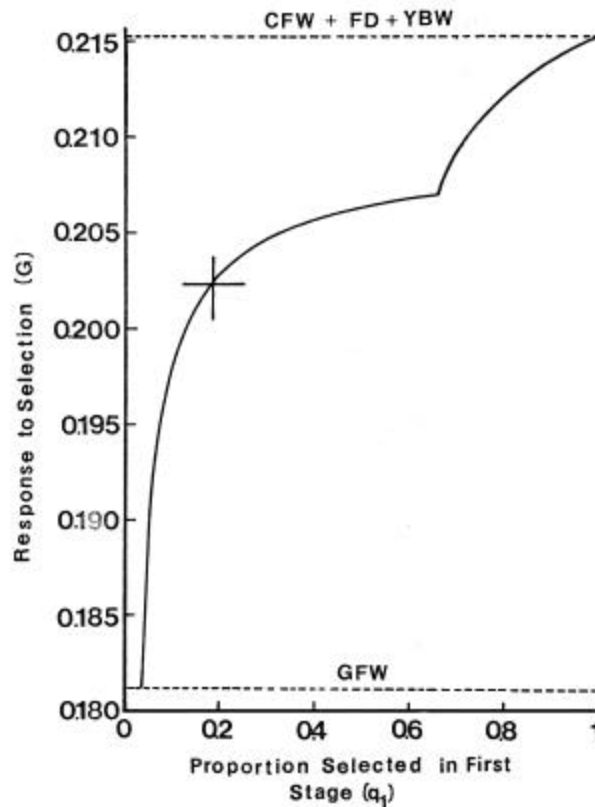
For illustration, suppose that in the example, males and females in the nucleus are selected on index I (CFW, FD, YBW). A proportion  $q_1$  of base females is selected on GFW, and subsequently a fraction  $q_{BFN}$  out of  $q_1$  is selected on I. In the example  $q_{BFN} = 1/28.8$  and  $q_{BFB} = 0.625$ . Then

$$D_{BFN} = s(q_1) 0.1592 + s(1 / 28.8 q_1) 0.3686 \sqrt{(1 - (0.1592 / 0.3686)^2 c)}$$

$$D_{BFB} = ((1 / 28.8 + 0.625) s(1 / 28.8 + 0.625)) 0.1592 - D_{BFN} / 28.8) / 0.625.$$

Figure 1 suggests that selecting about equal proportions in the two stages,  $q = \sqrt{q_{BFN}}$ , is an efficient procedure. Further results for two-stage selection of base females and nucleus males were reported by Mueller (1984).

**Figure 1: Response with two-stage selection of base females. The broken lines indicate responses when all replacements are selected on the first index (GFW) or the second index (CFW + FD + YBW). Response when selecting equal proportions in the two stages is indicated with the cross.**



## PROGENY TESTING

The possible value of progeny testing in open nucleus systems was considered by Rae (1976), who suggested that after nucleus born ram hoggets had been selected on fleece traits, a further selection could be made on fertility-related traits of their daughters in base flocks. A formal treatment of progeny testing in selecting for a single trait measurable in both sexes was given Mueller and James (1984) and for selection on arbitrary indices by Mueller (1984). The penalty for the increased selection accuracy is a longer generation interval. The higher gains achieved with fewer rams would demand use of artificial insemination, as would use of fewer nucleus rams. The best operational systems depends on available facilities. Any extra response due to changes in population structure or selection intensity should not be attributed to progeny testing as such.

## Response rate

Suppose a fraction  $q_1$  of young rams are selected on an index  $I_1$ , and are progeny tested, with a fraction  $q_{NMN}$  out of  $q_1$  being selected on an index  $I_2$  combining data in  $I_1$  with progeny means. The genetic differentials for base and nucleus males are

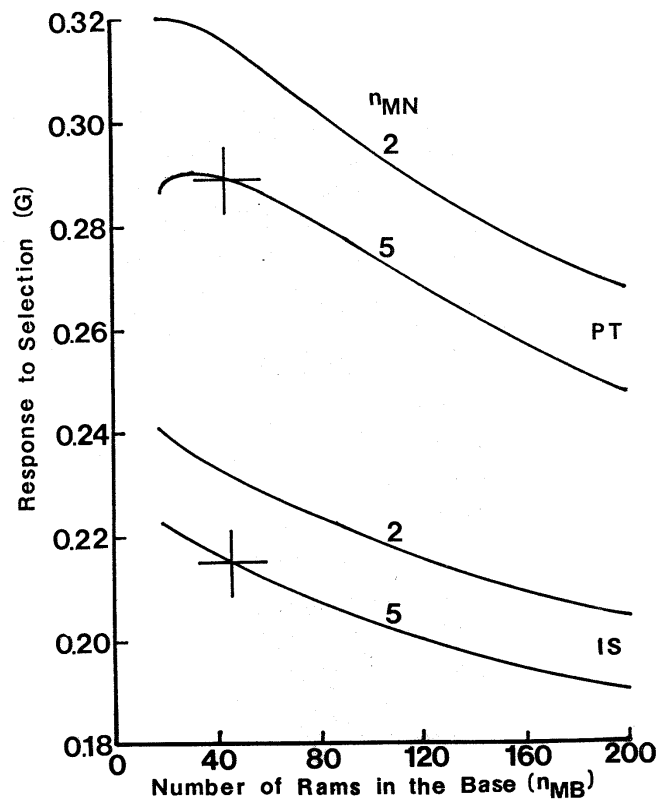
$$D_{NMB} = s(q_1) r_{HI1}$$

$$D_{NMN} = D_{NMB} + s(q_{NMN} / q_1) r_{HI2} \sqrt{(1 - r^2 c)}.$$

In the example,  $q_1 = 22.5 M_B$ , where  $M_B$  is the mating ratio (sires/dams) in the base, and  $q_{NMN} = 2.5 M_N$ , where  $M_N$  is the mating ratio in the nucleus, while the number of daughters per tested sire is  $0.4 / M_B$ . Suppose that in the example, young rams are selected as before on  $I_1$ , and ovulation rate (OVR) is measured on all females before first mating. Then nucleus rams are selected on an index  $I_2$ , using CFW, FD, YBW and daughters' OVR. Rams will be 2 years older at lambing in the nucleus so  $l_N$  is  $(4 + 3.5) / 2 = 3.75$  while  $l_B$  is still 2.75. Since ewes have OVR records they can be selected on an index  $I_1$  using CFW, FD, YBW and own OVR. Figure 2 illustrates the expected rate of genetic gain in a systems of 5000 ewes (500 in the nucleus) and either 2 or 5 rams in the nucleus, for varying numbers of rams tested in the base. Further examples of this type were given by Mueller (1984) and Mueller et al (1984). Clearly, progeny testing is advantageous in this example. As the number of young rams tested decreases, the accuracy of the test, and first-stage selection intensity increase, with a resulting increase in genetic gain. However, these structural changes also increases response to individual selection, a point often overlooked when comparing programs with and without progeny testing.

A critical point in the efficiency of progeny testing is the correlation between indices used at the two selection stages. As  $I_1$  is improved, relative superiority of  $I_2$  falls, and may not compensate for increased generation length. For example,  $I_1$  could be improved by use of dam's OVR, provided dam-offspring identification is practiced. Another possibility would be to consider half sister mean OVR in ram indices. This would normally require a large nucleus, but would avoid OVR measurement in the base, unlike progeny testing.

**Figure 2: Response with individual performance selection (IS) and progeny testing (PT) when different numbers of rams are used in the base ( $n_{MB}$ ) and, in the nucleus ( $n_{MN}$ ). When every ram is mated to 100 ewes results are indicated with a cross.**



### Inbreeding rates

With many more dams than sires in an open nucleus system, the effective population size  $N_e$  is given by (James, 1978):

$$1 / N_e = g^2 / (4 n_{MN}) + (1 - g)^2 / (4 n_{MB}).$$

When there is progeny testing, some of the  $n_{MB}$  test sires leave progeny in both nucleus and base, and this must be allowed for in calculating effective size. It can be proved that:

$$1 / N_e = g^2 / (4 n_{MN}) + (1 - g^2) / (4 n_{MB}).$$

Since  $(1 - g^2) < (1 - g)^2$  in open nucleus systems, progeny testing would give faster inbreeding if generation lengths were the same. Usually the generation length with progeny testing is much greater, and the inbreeding rate is lower than with individual selection. Results for the sheep example are given in Table 1.

**Table 1: Annual inbreeding rate  $(1 / 2 N_e) \times 100\%$ , in the sheep example with  $g = 2/3$  and  $n_{MB} = 45$ .**

$n_{MN}$	Progeny test	Individual selection
2	0.25	0.37
5	0.11	0.15

### Breeding objective and choice of program

Precise definition of a breeding objective is usually not critical, provided important traits have approximately correct relative weightings. Breeders sometimes disagree on the value of some traits, such as increased sheep fertility. Some argue that extra lambs involve considerable extra feed costs, while others assume no extra feed costs in grazing animals. Jones (1982) defined a breeding objective for Merinos which gave about half the weight to fertility traits which Ponzoni (1979) gave. Mueller et al (1984) investigated the design of progeny testing programs using OVR for improving either Jones' or Ponzoni's objective. Some results are shown in Table 2.

**Table 2: Rates of genetic gain for different programs.**

Objective	Progeny test	Individual selection
Ponzoni (1979)	0.29	0.22
Jones (1982)	0.28	0.30

Progeny testing is advantageous for Ponzoni's but not for Jones', objective. This illustrates the point made earlier about the relative efficiencies of the indices used at the two stages. The progeny test index was not sufficiently better for Jones' objective to outweigh the increased generation interval.

## DISCUSSION

In considering alternative measures to improve response in open nucleus systems, it is useful to collect the various results presented using our sheep example in Table 3. These are for Ponzoni's objective.

**Table 3: Comparison of responses in different programs.**

SELECTION CRITERIA			RESPONSE
BASES FEMALES	NUCLEUS FEMALES	NUCLEUS MALES	
GFW	GFW	GFW	0.093
GFW	GFW	I	0.167
GFW	I	I	0.181
GFW/I	I	I	0.202
I	I	I	0.215
$I_i$	$I_i$	$I/I_0$	0.289

All indices (I) include CFW, FD, YBW. To these are added: individual OVR in  $I_i$  and OVR of 40 daughters in  $I_0$ .

As a basis for evaluating the open nucleus structure, a sheep breeder selecting on GFW in a closed flock would gain at  $0.085 \sigma_H$ . The greatest impact is made by improved sire selection, for example using I rather than GFW, or I and  $I_b$  rather than I. measuring OVR in nucleus and base gave greatest gains of all. It should be pointed out that the same nucleus size and transfer rates, and flock structure were used for all programs. Ideally, these would be optimized for each program. However, such changes would have little effect on the results.

We have considered expect selection responses, but in practice genetic drift will lead to variable results in similar programs. Larger systems have a better chance of success (Nicholas, 1980). Over time, responses would decline as genes become fixed by selection on random drift, though this is a very slow process in large populations. But even in large populations the generation of linkage disequilibrium by selection (Bulmer, 1971) can lead to less than predicted progress. Mueller and James (1983, 1984) investigated these effects in open nucleus systems and showed that they could be neglected in designing systems, but that the usual equations (2) and (6) overestimate gains by 3 to 5% for traits with low heritability, or 20 to 25% for traits with high heritability. Predicted responses are also based on the assumption that all culling is on the nominated selection criteria, which may not be true in practice (Dodd and Delahunty, 1983).

Open nucleus systems can operate effectively with current methodology, but if pedigree recording and data processing facilities are available, the breeder may use more advanced procedures. For example, BLUP could be used to estimate actual genetic differences between groups from different parts of the system, thus accounting for random deviations from the expected pattern or response, estimating genetic trends in comparing animals or different ages, and allowing for effects of initial genetic mean differences in the early stages of the program (Rae and Anderson, 1982). Such developments are unlikely to occur in the near future in extensively managed systems, but may not be far off in intensive systems.

## **ACKNOWLEDGMENTS**

This work was done while J.P.M held a scholarship from the Instituto Nacional de Tecnología Agropecuaria INTA (Argentina).

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