STRUCTURED BREEDING PROGRAMMES

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INTRODUCTION

In most livestock breeds, genetic improvement is largely in the hands of a small proportion of all people owning the animals. The concentration of genetic control may be in the traditional form, such as in the sheep and beef cattle industries, where a large number of studs provide breeding animals for the commercial producers. It may be in the form of a few large breeding companies, as is the case in poultry, and may be the case in pigs in the not too distant future. It may take the form of large-scale progeny testing systems such as in dairy cattle. In all cases, the reason for such special breeding systems is that effective genetic improvement requires special effort, and the expense of running a selection programme can be recouped by the premium paid for breeding stock.

Within the stud section of the industry, there is usually further differentiation, with studs being subdivided into tiers, which are commonly referred to as elite studs and multiplier studs (Robertson and Asker, 1951). Within some breeds, such as the Australian Merino, there is a further division which cuts across this. Short and Carter (1955) showed that the Merino is divided into strains, and within these strains there are family groupings, each headed by a parent stud.

In the last twenty years, a different type of structure, which can be called an open nucleus breeding system (James, 1977) has become widespread. In contrast to the traditional system, in which genes (carried by breeding stock) travel in one direction only, from stud to commercial stock, in open nucleus systems there is a flow of genes back into the breeding nucleus from the commercial stocks.

What are the consequences of such structures for genetic improvement of livestock?

GENE FLOW

Since livestock improvement depends on changes in the frequencies of genes affecting important traits, it is the way in which a structure affects the flow of genes between different segments of a population which governs the influence of the structure on genetic change in the whole breed. We must therefore consider the gene flow which occurs in any such system when we seek to evaluate it.

Bichard (1971) gave a detailed discussion of the way in which genetic improvement is passed down in a hierarchical system from the elite breeding nucleus to commercial production units. Let us consider first an integrated system in a species with a high reproductive rate, such as in poultry breeding. Suppose there is an elite nucleus flock, and a multiplier flock to be produced by surplus nucleus animals, then the mean breeding value of the multiplier flock in any generation would differ from that of the nucleus only by the difference in breeding value between animals selected to produce the next nucleus generation and animals chosen to produce the next multiplier generation. If animals used to produce the multiplier were of average breeding value for their nucleus generation, there would then be a difference of one generation of genetic gain. For the same reason, there would be a lag of one generation of improvement between the multiplier flock and commercial stock, which would thus lag two generations behind the nucleus. Clearly, all parts of the system would be making genetic progress at the same rate. This simple case thus illustrates two important features of such structures: the system as a whole progresses at a rate determined by the nucleus; and there is a lag in the transmission of genetic gains between adjacent levels in the hierarchy.

In larger, slower-breeding species, such as sheep and cattle, multiplication cannot be carried out using surplus females from the higher layer, but separate populations are needed. The transfer of genetic gain is then accomplished through the males, males bred in the nucleus being used as sires in the multiplier, and males bred in the multiplier being used as sires of commercial animals. It turns out that the consequence of disseminating gains through sires only is to double the lag period, if average sires are used, while rates of gain are still the same as in the nucleus after an initial period in which there may be fluctuations. A further complicating factor with sheep and cattle, as distinct from poultry, is that generations overlap instead of being discrete. However, this does not alter the general conclusions.

In hierarchical systems it is not necessary that all sires in the multiplier are introduced from the nucleus, and some home-bred sires may be used. Also, the introduced sires may be selected as genetically superior to the average of the nucleus, and breeding females in the multiplier may themselves be selected. What are the consequences of these factors for genetic change in the system?

Suppose the rate of genetic progress in the nucleus is G per year, and a fraction w of the males used as multiplier sires come from the nucleus, the remaining (1 - w) being home-bred. Suppose the sires introduced from the nucleus have average breeding value D_M above the mean of the nucleus at the time of their birth, while the home-bred sires have a corresponding genetic selection differential of d_M. Multiplier dams have a genetic differential of d_F. The average age of introduced sires when their progeny are born is L_M, the ages for home-bred sires and dams being l_M and l_F. Then it can be shown (James, 1977) that if A is the lag between nucleus and multiplier,

$$A = [2\bar{l}G - wD_M - (1 - w)d_M - d_F]/w \qquad (1)$$

where $\bar{l}$ is the generation length in the multiplier and

$$\bar{l} = \tfrac{1}{2}[wL_M + (1 - w)l_M + l_F]$$

When all sires are introduced, this reduces to

$$A = 2\bar{l}G - D_M - d_F \qquad (2)$$

When no selection is applied to multiplier sires and dams, (1) reduces to

$$A = 2\bar{l}G/w$$

and shows that the more home-bred sires are used, the greater the lag. From a practical viewpoint, the question would be whether cost savings from having w less than unity would compensate for the increased lag. In reality, sires would be selected, and the question would be whether d_M could be large enough to offset the effect of reduced gene flow. Thus we should compare the lag values given by (1) and (2). The difference is

$$A_w - A_1 = [2\bar{l}G - d_M - d_F](1 - w)/w \qquad (3)$$

If the multiplier were to close the population and breed from home-bred sires and dams with genetic selection differentials d_M and d_F, its rate of gain would be $(d_M + d_F)/2\bar{l}$, assuming $\bar{l}$ would be unaltered. Thus the condition for reducing the lag by using home-bred sires is that the "home-bred rate of gain" should be greater than the nucleus rate of gain,

$$\frac{d_M + d_F}{2\bar{l}} > G$$

If this is true, use of home-bred sires will reduce the lag. Of course, if the multiplier could make more rapid progress by closing the population, it would be an advantage to introduce no sires at all, since the sires from the nucleus would act as a brake on progress. However, if only some of the sires are home-bred, they can be selected more intensely than if all are, so that although the condition for use of home-bred sires may be met when they are only a part of the sires used, use of all home-bred sires might not be justified. One could use the above equations to find an optimum value of w, if the quantities in the equation were known.

It should be noted that the equations given are for lags, which are affected by selection in the multiplier population. Selection in the multiplier has no long-term effect on the rate of gain when gene flow is unidirectional, only nucleus selection having such effects. The only effect of selection in the multiplier is to reduce the extent to which it lags behind the nucleus.

If the transfers from the multiplier to commercial producers follow the same pattern, the same equations can be applied to lags between these levels of the hierarchy. If there is no multiplier level, the equations would apply to lags between nucleus and commercial producers. These

equations have been used to analyse sire buying policies by James (1979a, 1980) and Ollivier and James (1986). They assumed all sires were introduced to a commercial unit, and that the relative profitability of the unit depended on the lag. Assuming sire prices were determined by breeding value, they considered what turnover rate of sires, and what price of sire purchased gave the best balance between sire purchase costs and value of production.

OPEN NUCLEUS SYSTEMS

With unidirectional gene flow, selection applied outside the nucleus has no long-term effect on genetic gain, but can reduce lags. If lags are not great, there will certainly be animals in the lower levels of the hierarchy which are genetically superior to some in the nucleus, and if they can be identified and used in the nucleus they will contribute to genetic gain. This is the basic reason for running an open nucleus system. Since males can usually be intensely selected, the lag is likely to be too great a handicap for males at a lower level, and even the best are unlikely to reach a level good enough for use as nucleus sires. However, when females cannot be intensely selected, the best from the lower level are likely to be good enough for use as nucleus dams. Thus we would expect open nucleus systems to be of most value when reproductive rates are low and selection intensity on the female side is not great.

Jackson and Turner (1972) analysed the rates of gain possible in an open nucleus system for sheep, while a more general analysis was made by James (1977), who confirmed and extended earlier results. James also pointed out that an open nucleus system would have lower rates of inbreeding than a closed nucleus system of similar size, and found by numerical calculation that in practical situations the rate of inbreeding would be approximately halved. This was confirmed when James (1978) derived an expression for the rate of inbreeding in open nucleus systems. The conclusions from these analyses were that under favourable conditions the rate of genetic gain in an open nucleus could be about 10% to 15% better than in a closed one, that about 5% to 10% of the population should be in the nucleus, about 50% of nucleus dams should be brought in from the base [i.e. the population outside the nucleus], and that all surplus nucleus females should be used as base dams. The optimum operating conditions could be varied somewhat without appreciable loss of response. In these analyses, it was assumed that selection criteria and accuracy were the same in nucleus and base.

If w and y are the fractions of base sires and dams born in the nucleus, v and x are the fractions of nucleus sires and dams born in the base, C_N and C_B are the selection differentials of nucleus and base parents, l_N and l_B are generation lengths in nucleus and base, the rate of gain and lag in an open nucleus system can be found as follows. Let

$$g = (w + y)/(v + x + w + y)$$

so that g is the fraction of all gene flows which are from nucleus to base. Then the annual rate of genetic gain is

$$G = (gC_N + (1 - g)C_B)/(gl_N + (1 - g)l_B) \qquad (4)$$

while the lag is

$$A = 2(I_B G - C_B)/(w + y) \qquad (5)$$

If n_{MN} and n_{MB} are the numbers of new sires used in nucleus and base each year, with n_{FN} and n_{FB} the numbers of new dams, the annual rate of inbreeding is

$$\Delta F = \frac{[g^2(\frac{1}{8n_{MN}} + \frac{1}{8n_{FN}}) + (1 - g)^2(\frac{1}{8n_{MB}} + \frac{1}{8n_{FB}})]}{[gI_N + (1 - g)I_B]^2} \qquad (6)$$

One advantage of using a breeding nucleus is that it can be managed with a view to maximising genetic gain rather than commercial production. Thus the age structure may be chosen to reduce generation lengths, though the use of young dams may reduce productivity, and it may be economic to measure and record more traits than in a population being used for commercial production. These practices make selection in the nucleus more efficient than selection in the base, and as a consequence reduce the value of opening the nucleus. Under these conditions, Hopkins (1978) showed that the greater effort in the nucleus produced more rapid gain and also increased the lag, with the result that the optimum fraction of females to be introduced from the base to the nucleus declined. In a further analysis of this question, Mueller (1984) studied the use of a range of different selection criteria in nucleus and base, and the use of two-stage selection, and the ways in which these influenced optimal designs. When selection criteria differ considerably between nucleus and base, there may be very little advantage in an open nucleus system, so that closing the nucleus may be recommended. However, each individual case would require separate consideration. Hopkins (1978) and Mueller (1984) should be consulted for more detail.

Open nucleus systems can be used in any type of breeding operation, such as a traditional Merino stud, where the breeder may set aside a sire breeding nucleus within which all rams who are candidates for selection as sires are born, but in which females from the rest of his flock may be used as dams. A nucleus may be set up to provide potential sires which are progeny tested in the base, the best selected on progeny test being used as nucleus sires. Rae (1976) suggested use of such a system to improve a single trait such as clean fleece weight. Other examples were given by Mueller (1984), Mueller and James (1984b) and Mueller, Piper and James (1984). The critical question in the use of progeny testing is whether the extra information obtained through progeny testing allows a sufficient increase in selection accuracy to offset the greater generation length. For example, Mueller, Piper and James (1984) considered the use of progeny testing for ovulation rate of daughters in addition to selection of rams on individual wool and body traits. They showed that if the selection objective were that of Ponzoni (1979), progeny testing would be superior, but that if the objective were that of Jones (1982), progeny testing would slow progress. Modern dairy cattle breeding systems, in which all young bulls which are progeny tested are sons of

elite bulls of the previous generation, can be regarded as open nucleus systems. The nucleus consists of bull sires and bull dams, and all sires are then bred in the nucleus. However, bull dams may be selected from the general cow population. Thus the programme fits the specifications of an open nucleus system, but because of the way it is organised, with the breeding nucleus not at one location, it is not usually considered in this light. In addition, the use of AI and BLUP technologies means that breeding values of animals in different herds can be directly compared, resulting in a simple final method of selection on estimated breeding value. So there is no particular value in regarding it as an open nucleus system. Most interest in open nucleus systems is shown by cooperative group breeding schemes.

GROUP BREEDING SCHEMES

Much of what has already been presented applies to group breeding schemes, but there are a few points of special interest in these programmes. The first is that where there are very many flocks in the base, it may seem unrealistic to treat the base as a unit, as has been done in previous discussion. The equations given above for rates of gain and lag can readily be adapted and, as shown by Mueller and James (1984b), the appropriate equations are

$$G = (C_N + \Sigma C_{Bi}(1 - g_i)/g_i)/(l_N + \Sigma l_{Bi}(1 - g_i)/g_i) \quad (7)$$

and

$$A_i = 2(l_{Bi}G - C_{Bi})/(w_i + y_i) \quad (8)$$

where the i subscript refers to the ith flock, and Σ denotes summation over all flocks.

Again we see that the rate of progress is eventually the same in all flocks, but that some flocks may have different lags from others. These equations apply to long-term changes. In the short-term, the results may be rather different. For example, suppose one contributor has, through efficient selection in the past, raised the breeding value of his flock to a value well above the nucleus. He could expect his flock's mean breeding value to decline for some years before it started to rise again (Guy and Steane, 1980). Eventually it would rise at the same rate as the others, but would now lag behind the nucleus. Such a person would need to consider how long it would take for the benefits of group membership to accrue. In practice, a great difficulty in making such decisions is the lack of accurate estimates of differences in flock mean breeding values. Some guidelines for getting such estimates were given by Roberts (1979) and James (1979b).

In some group breeding schemes the main virtue of the system may be the increased population size and consequent reduction of inbreeding. This will be the case only when the nucleus is not very large. If the nucleus consists of, say, 1000 to 2000 ewes, any further increase in size produces only marginal reduction in inbreeding. As shown by James (1977) it is essentially the size of the nucleus which matters, the relative size of the base being of little significance. Indeed, a large base may bring problems. The larger the base, the more likely is it that a wide range

of environments are represented, with an increased chance of genotype-environment interactions. These, if they occur, will reduce the efficiency of selection. Problems of organisation are also likely to arise. The extent to which these can be overcome will depend on the managerial abilities of the group. Even small group breeding schemes will function successfully only with good management.

Apart from the genetic advantages of the open nucleus structure, which may sometimes be very small, there are other advantages of group breeding schemes.

Perhaps most important is that in a cooperative system the breeding goals can be defined by the members to meet their own needs. Members of a cooperative have their future in their own hands, instead of relying on others to produce the genetic improvement which they will depend on for increased productivity. In addition, the mere fact that breeding goals have to be defined may be a great help in clarifying objectives which had been only vaguely perceived beforehand.

CONCLUSION

To make rapid genetic gains, it is often necessary to use special methods, such as intensive measurement and recording, or keeping of pedigrees, and computations, which would not be justified in a population used for commercial production. In these circumstances, a breeding nucleus which can recoup expenses through sale of improved breeding stock (or gametes) is a rational solution. The breed has then to adopt a structure which leads to efficient dissemination of improvement. It is possible to achieve rapid gains and short lags either with traditional stud systems, with group breeding schemes, or with integrated breeding companies. In reducing lags, it is important to turn over generations quickly, to select replacements as effectively as possible, and to choose optimum rates of gene flow. With appropriate design, each type of organisation will be appropriate to some breed improvement programmes.

REFERENCES

Bichard, M. 1971. Anim.Prod., 13: 401-411.

Guy, D.R. and Steane, D.E. 1980. 31st Annual Meeting, EAAP.

Hopkins, I.R. 1978. Anim.Prod., 26: 267-276.

Jackson, N. and Turner, H.N. 1972. Proc.Aust.Soc.Anim.Prod., 9: 55-64.

James, J.W. 1977. Anim.Prod., 24: 287-305.

James, J.W. 1978. Acta Agric.Scand., 28: 387-392.

James, J.W. 1979a. Proc.Aust.Assoc.Anim.Breed.Genet., 1: 44-45.

James, J.W. 1979b. Proc.Aust.Assoc.Anim.Breed.Genet., 1: 47-48.

James, J.W. 1980. Ann.Génét.Sél.Anim., 12: 33-47.

Jones, L.P. 1982. in 'Future developments in the genetic improvement of animals.' ed. J.S.F. Barker, K. Hammond and A.E. McClintock. (Academic Press: Australia) pp.119-136.

Mueller, J.P. 1984. Génét.Sél.Evol., 16: 103-119.

Mueller, J.P. and James, J.W. 1984a. Anim.Prod., 38: 1-8.

Mueller, J.P. and James, J.W. 1984b. Proc. 2nd World Congr. Sheep and Beef Cattle Breeding. pp.204-213.

Mueller, J.P., Piper, L.R. and James, J.W. 1984. Proc.Aust.Soc.Anim.Prod., 15: 484-486.

Ollivier, L. and James, J.W. 1986. Journées Rech.Porcine en France, 18: 253-260.

Ponzoni, R. 1979. Proc.Aust.Assoc.Anim.Breed.Genet., 1: 320-336.

Rae, A.L. 1976. in 'Sheep breeding.' ed. G. Tomes, D.E. Robertson and R.J. Lightfoot. (WAIT: Perth) pp.154-164.

Roberts, E.M. 1979. Proc.Aust.Assoc.Anim.Breed.Genet., 1: 48-50.

Robertson, A. and Asker, A.A. 1951. Emp.J.Exp.Agric., 19: 113-130.

Short, B.F. and Carter, H.B. 1955. CSIRO Bulletin No. 276.