FUTURE CHALLENGES IN SHEEP BREEDING RESEARCH

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INTRODUCTION

It is always timely for research organisations to devote some of their intellectual capacity to consideration of the future challenges that may arise in their particular areas of interest. Good research planning involves anticipating the future needs of industry and setting in place the required programs, human resources and technical infrastructure to service those needs. This process implies stable long term funding for core research activities, though shorter term funds may be utilised for tactical research purposes. However, it is vital to restrict the proportion of short term funding and to maintain a proper balance between fixed costs (salaries, maintenance etc.) and operating monies in the core funded component. Such a strategy ensures the necessary flexibility that is required if the organisation is to be viable and achieve its long term goals of scientific excellence and service to industry.

In attempting to identify future challenges in sheep breeding research it is necessary to be mindful of the situation currently faced by all animal breeding research planners. They must resolve the competing demands of those advocating further refinement of traditional quantitative genetic approaches and those championing the newer molecular genetic technologies. In writing this review I have attempted to be objective but the areas highlighted are a personal perspective and are not intended as an exhaustive list. There may be omissions, but I hope the serious ones have been kept to a minimum.

DEFINITION OF BREEDING OBJECTIVES

In classical selection index theory, a breeding objective (H) is defined as the sum of breeding values for economically important traits weighted by the relative economic value of a unit change in each of the traits. Thus

$$H = a_1T_1 + a_2T_2$$

would be a breeding objective incorporating traits T_1 and T_2 with relative economic weights a_1 and a_2. The traits included in the breeding objective should be all those that affect returns and costs and there has been considerable debate about the relative merits of different accounting approaches (ratios of economic efficiency or profit equations). A long standing difficulty has been that the relative economic values depend on the perspective taken (producer, investor, consumer) and on the accounting approach. This has recently been resolved by Smith et al. (1986) who showed that if all costs are regarded as variable, and any changes

which can be matched by rescaling the enterprise are excluded, the profit equation gives the same economic weights for all perspectives.

Definitions of breeding objectives for sheep which properly account for returns and costs are still hampered by lack of variance-covariance estimates for food intake. However, a new technique which utilises intra-ruminal slow release devices containing chromic oxide to estimate daily faecal output from individual grazing sheep has recently been developed. Using this technology, Lee et al. (1990) have obtained a preliminary estimate for the heritability of food intake for grazing Merino ewes (based on the mean of 5 measures) of 0.26 $\pm$ 0.16. This is a start, but a great deal more research is required to develop precise lifetime variance-covariance estimates for food intake and other economically important traits of grazing sheep across a range of environments.

Disease resistance traits clearly influence costs of production but their inclusion in breeding objectives can present special problems. These arise because the scale on which disease resistance is measured biologically often has no clear economic interpretation. For example, resistance of sheep to internal parasites is usually assessed by counting parasite eggs in sheep faeces. However, there is no obvious way of linking faecal egg counts to costs of parasite treatment and thence to estimation of a relative economic weight for the resistance trait. This dilemma is common to many disease traits and some new thinking is required in order to include them in breeding objectives for sheep managed so as to minimise the effects of disease.

It is becoming clear that for some traits which have a number of expressions over the economic lifetime of a sheep, the genetic correlation between expressions is not unity. This means that it may be necessary to include all expressions as different traits in the breeding objective or at least separate the early and later expressions. The advantages of including additional expressions of a trait in the breeding objective include more accurate prediction of genetic responses, more appropriate economic evaluation of those responses and of the merits of alternative selection criteria. A recent paper by Atkins (1990) confirms the benefit of including lifetime expressions of fleece weight and fibre diameter in breeding objectives for Merino sheep. In the same report, low precision of parameter estimates for reproductive traits due to sub-optimal experimental design for those traits, meant that the significance of genetic variability across expressions could not be assessed.

Finally, it is clear that for some sheep production systems there will need to be an increase in the number of traits included in breeding objectives as product quality considerations assume increasing marketing importance. Relevant examples include carcase quality traits in meat sheep production systems and additional traits specifying the finer detail of wool quality (e.g. style, bulk, resistance to compression, colour) in specialist wool breeds. Research will be required to estimate relative economic weights and appropriate variance-covariance matrices for these additional product quality traits.

EVALUATION OF SELECTION CRITERIA

The need to re-evaluate the merits of alternative traditional selection criteria in respect of lifetime productivity based breeding objectives has already been identified. Such evaluations should also incorporate assessment of the merits of including information from additional relatives or from additional records.

The search for "marker" or indicator traits (physiological, immunological, biochemical) which may have merit as indirect selection criteria for improving intractable (sex limited, all or none expression, low heritability) economically important characters should undoubtedly continue. The necessary conditions for such indicator traits to be of value are well understood. When both traits can be measured in both sexes and

the selection intensities that can be applied for the indicator and direct trait are the same, the response to indirect selection will be greater when

$$r_g h_i / h_d > 1$$

where r_g is the genetic correlation between the traits
h_i is the accuracy of selection for the indicator trait
h_d is the accuracy of selection from the direct trait.

When the direct trait can be measured in only one sex (e.g. litter size) but the indicator trait in both (e.g. plasma FSH), or where realised selection intensity for the indicator trait (continuously distributed) is greater than for the direct trait (low incidence, all or none expression), the relative response from indirect selection will be further enhanced. Regardless of its merit as a selection criterion for improving a single character objective, the real value of an indicator trait will usually need to be assessed as part of a multi-trait selection criterion for improving a multi-trait objective. This assessment should incorporate appropriate cost benefit analyses.

BREEDING PROGRAM STRUCTURE AND MATING SYSTEMS

In common with most animal breeding industries, sheep breeding structures are generally hierarchical in form. The major studs or ram breeders are at the tops of pyramids and gene flow is generally downward through one or more tiers. The advantages of open nucleus schemes, in which superior animals from lower tiers are permitted to migrate upwards are well documented (James, 1977). Many such schemes, involving two or three contributory tiers are now in existence in most major sheep producing countries.

A significant recent development in Australia has been the migration or common use of genetic material between otherwise separate open nucleus schemes or studs. This will give rise to increased genetic connectedness which, when combined with additional measurement and appropriate mixed model (BLUP) procedures for genetic evaluation, should increase overall rates of genetic progress by allowing truncation selection across flocks on the basis of estimated breeding values.

A recent paper by Kinghorn and Shepherd (1990), discusses a comprehensive approach to breeding program design which suggests that the way forward is to incorporate into a unified decision making process most of the elements of importance in animal breeding (selection value, assortative mating, connection, lifetime value, parameter estimation, measurement strategies, crossbreeding value, running costs, inbreeding, reproductive manipulation, exploiting major genes, and risk). The authors admit that "a grand unified theory is currently elusive" but attempts to develop such a theory should clearly be seen as a major future challenge.

BREEDING FOR DISEASE RESISTANCE

Some important parasites of sheep are not presently able to be controlled by reliable vaccines. Most internal and external metazoan parasites fall into this category and current control procedures rely heavily on chemotherapy to reduce production loss. The development of drug-resistance in parasite populations is a common phenomenon and this has led to increasing interest in genetic manipulation of sheep their resistance to such parasites. In Australia and New Zealand, real progress has been made in breeding sheep that are resistant to common helminth parasites (Woolaston, 1990; Baker et al, 1990). Work is in progress in relation to other important diseases such as foot-rot and fly-strike, but much more is required,

especially in light of the increasing pressure for reduced use of chemicals in all aspects of agricultural production.

UTILISATION OF NEW REPRODUCTIVE TECHNOLOGIES

The theoretical advantages of new (and not so new) reproductive technologies are well documented but, with the possible exception of AI, they have so far had little impact on genetic improvement of sheep. Increasing use is being made of frozen semen AI especially since the advent of intra-uterine laparoscopic insemination procedures (Killeen and Caffery, 1982). With this technique, fertility levels are equivalent to those obtained with cervical insemination using fresh semen, though the costs are considerably higher. Increases in genetic gains within flocks would only be expected to be marginal and may be partially offset by increased rates of inbreeding. The major benefits in the sheep industry will come from common use of sires across flocks leading to the possibility of across flock genetic evaluation and in the servicing of diffuse elite nuclei. Research is urgently required to improve fertility following cervical insemination with frozen-thawed sheep semen.

The theoretical advantages of MOET schemes are clear (Smith, 1986) but care needs to be exercised to ensure that effective population sizes are such that inbreeding is kept to acceptable levels and long term selection gains are not compromised. Recent studies of inbreeding in selected populations clearly demonstrate that the rates are higher than for unselected populations and higher than predicted by the classical Sewall Wright models (Wray and Thompson, 1990). The theoretical advantages of MOET schemes may need to be reassessed especially for reproductive traits which are likely to be more susceptible to inbreeding depression.

The ability to preselect the sex of offspring, by effective separation of X and Y sperm, has been shown to have the potential to increase rates of genetic gain in the dairy industry by up to 15% (Van Vleck, 1981). Significant benefits might also be expected in the sheep industry if reliable semen sexing were available. The recent report by Johnson et al (1989) confirms live births from rabbit X and Y sperm separated according to DNA content. There is no reason to doubt that this technique could successfully be adapted for ovine semen and research should be directed to achieving that purpose.

It is now possible to clone individuals by division of early embryos. Aside from increasing the number of progeny per dam, this gives rise to the possibility of more accurate evaluation of a genotype. However, for the same total number of animals measured, the resultant increase in heritability must be balanced against either a reduction in selection intensity or an increase in levels of inbreeding (James, 1988). The value of cloning for sheep will be increased when embryonal stem cell culture and nuclear transplantation techniques are further developed for this species (Clark, 1990). It will then be possible to culture embryonal stem cell clones from highly selected parents, transplant and grow representatives of each clone to the measurement stage, and then select the best clones to generate the next round of breeding stock. Once again, for a fixed number of measured animals there will be trade-offs between increased accuracy of selection and reduced selection intensity or reduced effective population size. Embryonal stem cell culture techniques for sheep are in the early stage of development (Notarianni et al 1990) but research will undoubtedly continue because of their likely future importance in creating transgenic animals (Clark, 1990).

GENETIC ARCHITECTURE OF QUANTITATIVE TRAITS IN SHEEP

Genes affecting wool colour and hornedness have been known for some time but until recently there have been few reports of individual genes that influence quantitative traits. However, since the discovery of the

Fec^B gene which markedly increases ovulation rate, there have been reports of similar genes in a number of other breeds (Piper and Bindon, 1988). The statistical methodology for detecting the segregation of individual quantitative genes has improved but the probability of detecting genes with effects less than one standard deviation is small. One of the major challenges for the future will be to improve the statistical and experimental methodology so that attempts to map quantitative trait loci (QTL) of sheep through their linkage to DNA sequence polymorphism markers, can be made much more precise. In the shorter term, such developments will improve the efficiency of marker assisted selection (MAS) and undoubtedly lead to its increased utilisation in practical sheep breeding programs (Smith and McMillan, 1989).

TRANSGENICS

The process of creating transgenic animals by directly transferring a gene into the germline of a target breed offers exciting new possibilities for genetic manipulation of productivity in all farm animals including sheep. If relevant genes can be identified, isolated and cloned, they can be transferred individually to the target breed in one generation.

At the present time, this form of gene transfer in sheep is effected by direct injection of several hundred copies of a gene into the pronucleus of an early embryo. The proportion of injected eggs that eventually develop into transgenic offspring is low and averages around one per cent (Clark, 1990). The technique is in the developmental phase but improvements in embryo production procedures (e.g., in vitro fertilisation and in vitro maturation) and in gene transfer technology (e.g. use of retroviral vectors, embryonal stem cell culture techniques) are projected to increase to increase its efficiency. Techniques for inactivating or removing existing genes (e.g. anti-sense mutants, gene shears) are being developed and will be required for many transgenic applications. A great deal of research remains to be completed before this technology will be widely utilised to improve productivity in domestic sheep populations.

CONCLUDING REMARKS

The classical models of quantitative genetics, which are based on statistical abstractions, have served the sheep industry well and substantial improvements in productivity have been achieved. In the future we will need to become much more precise and discuss genetic variation in terms of genes rather than statistics. As stated by the late Alan Robertson in 1967, our aim must be to provide a description of the genetic variation in any trait in terms of the number of genes affecting that trait (or controlling 80% - 90% of the variation), the distribution of allele effects and frequencies, the type of gene action (additive, dominant, epistatic) the linkage relationships among the loci and their correlated effects on other production traits and fitness. It is clear that we have no shortage of challenges for the future.

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