SMALL RUMINANT BREEDING PROGRAMMES FOR MEAT: PROGRESS AND PROSPECTS

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INTRODUCTION

Sheep and goats were domesticated 12,000 years ago in Asia. Since then we have selected them knowingly or otherwise to fit the attributes of our husbandry systems and local environments and to yield products we deem important. Although modern tools have improved our capacity to make genetic change, these basic goals have changed little over time. Small ruminants make a significant contribution to world needs for food, particularly meat. Grasslands account for over 30% of the global land surface and small ruminants provide high quality foods from such lands that are largely unsuitable for crop production. With human populations expected to increase by one-third in the next 20 years, the contribution of small ruminants will need to grow (Bradford *et al*., 1999; Holst, 1999).

Our undertaking is to discuss progress and prospects in breeding programs in sheep and goats for meat production. The number and reproductive competency of breeding animals are key determinants of total output, as are efficiency gains from crossbreeding, but those topics are beyond the scope of this paper. We focus on characteristics of within-breed selection for meat production, including the traits to be improved (the breeding goal), ways they can be measured or predicted (the selection criteria), and experiences with their amalgamation into selection indices. Even where goals and criteria are defined well, structural and biological constraints slow genetic progress in small ruminant breeding programs. New technologies allow greater latitude to overcome these constraints. Among these are molecular genetic techniques, some of which have allowed identification and use of single genes with major affect on muscularity (e.g. Callipyge) and reproductive rate (e.g. Booroola). As molecular methodologies are discussed elsewhere, we will not expand upon them here. We will focus on the design of group breeding schemes, particularly sire referencing schemes, which provide a mechanism to overcome structural constraints in breeding programs.

SELECTION

Biological considerations. Strategies to alter the composition of the carcass act either through direct effects on the composition or indirect effects on the size of the animal at maturity (Fitzhugh and Taylor, 1971; Thompson, 1990). The two effects may be linked. Growth waves or gradients in the tissues of the body exist and follow a specified order: brain, bone, muscle and then fat (Hammond, 1940). At each stage of growth, each of these tissues will have matured to a different extent. If live weight at maturity is increased, at a given immature weight, the earlier maturing tissues such as lean will make up a greater proportion of the body.

As a corollary, at a constant level of fatness, lambs sired by breeds of larger mature size produce heavier carcasses (McClelland *et al.,* 1976; Lewis *et al*., 1996).

Increasing mature weight or size, however, is not necessarily a panacea for improving efficiency of meat production in small ruminants. Shelton (2000) emphasized that ewe productivity (net reproductive rate) is the major factor affecting efficiency of meat production, and there are concerns that selection for size can adversely affect fitness and reproductive success. Lasslo *et al*. (1985) reported an increase in prolificacy with selection for live weight in sheep. However, these gains were offset by a reduction in fertility and lamb survival. There also is a tendency for larger breeds to have an above-average food intake for their size at early stages of growth (Thonney *et al*., 1987). Similar findings were reported for Merino sheep selected for heavier weaning weight (Thompson *et al*., 1985b). For animals of different mature weight, large animals generally take longer to reach the same stage of maturity for live weight, and consume more food in the process (Taylor, 1980). In dam lines, and where fodder is in limited supply, restricting increases in live weight is often desirable.

Potential breeding goal. Breeds tend to be similar in carcass composition when compared at similar degrees of maturity (McClelland *et al.,* 1976; Taylor, 1980). However, there is evidence of variation in fatness at maturity and rate of maturing in fatness (Butterfield *et al*., 1983, Thompson *et al*., 1985a, 1987). Although these are biologically useful concepts, they are difficult to apply to within-breed selection in practice. More practical selection objectives are to alter the rate of gain of lean tissue to an immature weight, or to alter the proportion of lean in the carcass at an immature weight (Simm, 1992). Such objectives are particularly relevant in sire breeds used in structured crossbreeding systems. Depending on the breed and production environment, mature size may be constrained or allowed to increase.

Besides carcass leanness, conformation is considered an indicator of carcass quality as 'better conformed' carcasses can attract higher financial returns. Shorter blocky carcasses are perceived to have higher lean to bone ratio and increased muscle thickness at the same carcass weight, although the association appears weak (Abdullah *et al*., 1993; Purchas and Wilkin, 1995) In some cases, higher conformation carcasses have been shown to be fatter (e.g. Lewis *et al*., 1996; Jones *et al*., 1999). Objective measures that are independent of size or live weight have been proposed to distinguish variation in muscle shape from fatness (Purchas *et al*., 1991; Jones *et al*., 2002b). Such measures may also detect differences in muscle shape in different regions of the carcass (Jones *et al*., 2002b), as some breed variation in muscle weight distribution has been reported (Thonney *et al*., 1987). Still, in contrast to carcass composition and weight, the economic importance of including shape in the breeding goal is less clear.

In future, eating quality attributes may need to be considered in the breeding goal. The polygenic inheritance of eating quality is not well understood. Still differences in cooking loss, muscle color, tenderness and juiciness have been detected between breeds of sheep and goats (Swan *et al*., 1998; Dhanda *et al*., 1999) although not universally (Esenbugaa *et al*., 2001). As consumers discriminate between foods based on ease of preparation and eating satisfaction, organoleptic and cooking properties may need to be considered in the goal.

Concern over food safety, including zoonoses, and production methods are affecting consumer's perceptions as to the wholesomeness and acceptability of foods. In parts of Europe these concerns have resulted in a surge in demand for high welfare, organically grown foods (including meats), which undoubtedly will lead to greater emphasis on animal health and fitness within breeding programs for meat production (Conington *et al*., 2002b). As there is evidence of genetic variation for disease resistance for important diseases (Mavrogenis *et al*., 1995; Bishop *et al*., 1996), there is opportunity and impetus to select for resistance. Selection for single loci (genes) that affect disease resistance is already underway [e.g. the prion protein (PrP) locus affecting scrapie resistance], although the pleiotropic effects of such loci require better understanding (Prokopová *et al*., 2002).

Selection criteria. As most breeding programs for meat focus on carcass leanness, the selection criteria usually include live weight and ultrasound measurements of fat and muscle depth, and to a lesser extent muscle area. More recently, X-ray Computed Tomography (CT) has been introduced to sheep breeding programs to allow more accurate *in vivo* measure of carcass composition (Young *et al*., 1996, 1999). CT offers substantial scope to accelerate genetic progress in lean meat production (Simm, 1992; Jopson *et al*., 1997). It also allows measure of other carcass attributes such as muscle shape and distribution (Jones *et al*., 2002a), and the depletion-repletion of tissues from body depots (Lambe *et al*., 2001, 2002) where deemed important (e.g. when decreasing carcass fat may compromise maternal ability).

Heritabilities are moderate to high for weight and ultrasonically measured traits in meat and dual-purpose breeds of sheep (e.g. Fogarty, 1995), but are somewhat lower in at least Boer goats (Schoeman *et al*., 1997). Recently, we have estimated heritabilities and genetic correlations for live weight, ultrasound muscle and fat depth, and lean and fat weight (as predicted from CT) at 150-days of age for three terminal sire breeds in Britain. Although our estimates largely align with those reported elsewhere, heritabilities of lean (0.46) and fat (0.39) weight were somewhat higher than expected, and fat depth and lean weight were genetically uncorrelated (0.01 to –0.10) which is advantageous.

Selection indices. The economic performance of small ruminants depends on several traits. Over the past 15 years economic selection indices have been used increasingly in sheep breeding, but to a lesser extent in goat breeding, to objectively weight different attributes of candidates for selection. Although estimates of genetic and phenotypic parameters are increasingly available for construction of indices, derivation of economic values for the traits in the breeding goal is problematic (e.g. Smith *et al*., 1986; Simm, 1992). This is largely because of poor and inconsistent market signals, complicated by ambiguity as to the end-user for whom the index is designed. One approach is to assess how various combinations of relative economic values (REV) affect response in goal traits. Simm and Dingwall (1989) did this to obtain REV of +3 for lean weight and –1 for fat weight for an index optimizing gains in lean growth rate; the selection criteria were live weight and ultrasound muscle and fat depth. Recently, Conington *et al.* (2000) used a bio-economic approach to obtain economic values for indices in hill breeds of sheep; doing so allowed the costs and returns of production systems to be linked to changes in genotypes and pastoral systems.

The value of CT measures as selection criteria has already been introduced. As CT is expensive relative to ultrasound, it is not practical to CT scan all candidates available for selection. However, much of the benefit of CT can be obtained at a fraction of the cost by the use of two-stage selection, where most animals are scanned ultrasonically with only those of higher genetic merit scanned by CT. The optimization of such two-stage selection schemes depends on balancing the cost of CT with the greater genetic gain that can be achieved. Research in New Zealand (Jopson *et al*., 1997) has shown that for a large nucleus breeding scheme (1,400 ewes), economic returns were maximized when all lambs in the nucleus were ultrasonically scanned and the best 13% CT scanned. At the Scottish Agricultural College (SAC), we recently predicted genetic response and economic returns for lean growth rate from two-stage selection. We modeled the three largest breeding schemes for specialized meat sheep in the UK (the Charollais, Suffolk and Texel sire referencing schemes). These schemes vary in number of ewes bred (2,000 to 6,100), number of stock sires used (130 to 340), average number of lambs recorded per ewe (1.1 to 1.3) and genetic co-variation for the *in vivo* predictors of carcass traits. As with Jopson *et al.* (1997), our best strategy was to ultrasound all recorded lambs but to CT scan only a proportion of ram lambs. When the optimal number of ram lambs were CT scanned in a scheme, genetic progress for lean growth rate increased by 16 to 32% over that for ultrasound alone. Economic returns (discounted over 20 years) exceeded costs when 10 to 25% of rams were CT scanned, although the greatest economic returns were achieved when 10 to 15% were CT scanned. Depending on the dynamics of the particular breed, expected cumulative net returns differed by over four-fold between breeds.

Response to selection. A number of experimental sheep lines have been established to test selection strategies for carcass composition traits. In NZ, selection was for divergent live weight-adjusted ultrasonic backfat depth (McEwan *et al.,* 1989; Morris *et al.,* 1997). Two UK experiments involved selection on an index designed to alter body composition at a constant live weight (Cameron and Bracken, 1992; Bishop, 1993). An economic index (Simm and Dingwall, 1989) was used at SAC to select Suffolk sheep for lean growth rate beginning in 1985. A selection and control line were established. After 9 years, the selection line weighed 4.9 kg more and had 1.1 mm less fat depth and 2.8 mm more muscle depth (as measured by ultrasound) than its control. Those responses are between 7 and 15% of the overall means for these criteria (Simm *et al*., 2002). In these and other experiments approximate annual rates of change in index score, or weight-adjusted backfat depth, are about 2% per annum. That is close to the maximum expected for the traits and flock sizes concerned.

Whilst measuring trends in components of an index is informative, achieving response in the selection objectives is the ultimate goal. After 9 years of selection in the SAC experiment, we measured the carcass composition of lambs over a wide range of weights. Selection line sheep produced carcasses with 23% higher lean to fat ratio as compared to the control line at all weights. Rams from the selection line grew 19% faster and were 17% more efficient than those from the control (Lewis *et al*., 1999, unpublished). In other experiments where carcass composition was measured directly (e.g. Bennett *et al*., 1988; McEwan *et al*., 1989), selection for reduced ultrasonically measured backfat depth resulted in reduced subcutaneous fat depth in the carcass. Proportions or weights of fat in other depots also decreased as expected given moderate genetic correlations between fat proportions in different depots (Wolf *et al*., 1981).

Environmental sensitivity. In within-breed selection programs, animals are often reared under more favorable conditions than their commercial counterparts. Thus the persistence of selection response under different feeding systems is important. When assessing response to selection in the SAC Suffolk flock, we therefore considered several feeding regimes. One regime was to restrict the level feeding of the high protein (188 g/kg DM CP), high energy (11.9 MJ/kg DM ME) ration fed during the selection phase. When fed at about half *ad libitum* intake, growth rate was reduced by 47% and feed efficiency by 19% in the selection line with virtually no difference in growth rate or efficiency between lines; the reduction in performance was substantially less in the control line, particularly for efficiency (4%). Thus performance in the selection line was more sensitive to level of feeding than in the control. Despite this sensitivity, the higher lean to fat ratio in selection line persisted regardless of feeding level. Thus progeny from lines selected for lean growth rate are expected to yield leaner carcasses across a wide range of finishing systems (Lewis *et al*., 1999, unpublished). This expectation has been confirmed in grass-reared crossbred lambs sired by high and low index rams from the SAC flock (Lewis *et al*., 1996; Simm and Murphy, 1996).

Evidence of environmental sensitivity in small ruminants has been documented elsewhere. Hohenboken *et al.* (1988) showed that a line of Romney ewes selected for overall productivity was more stable (less sensitive) to changes in stocking density, sward composition and selenium supplementation then industry Romney and Coopworth ewes. Bishop *et al.* (1996) reported substantial interactions for live weight and ultrasound traits in lambs from two genotypes of Scottish Blackface sheep depending on whether their rearing environment was relatively intensive or extensive. They concluded it would be inefficient to base selection decisions on lamb performance in intensive environments for extensive environments.

SIRE REFERENCING SCHEMES

In many countries, the average size of flocks (and herds) is small with little scope for intensive within-flock selection. Furthermore it is not simple to select animals from other flocks to overcome the constraint of small size as they often differ in husbandry. This problem has been overcome through cooperative breeding schemes. Nucleus breeding scheme are likely best known (e.g. James, 1977) but more recently sire referencing schemes (SRS) have gained popularity. This likely is because SRS entail fewer financial and legal responsibilities among members since a co-owned nucleus unit is not required. In SRS genetic links are created among flocks by mutual use of some specific rams (reference sires). These connections allow equitable across-flock genetic evaluations, offering a larger pool of candidates for selection for some collective goal. In some ways SRS are no more than a means to an end - they create genetic links that would occur naturally if AI in small ruminants were as common as that in dairy and beef cattle. However, optimal design of these schemes can also produce benefits in terms of rates of improvement.

The original design of SRS was based on expected accuracies in progeny testing schemes given the size of half-sib families. More recently we used computer simulation to study three factors in the design of these schemes in terms of their affect on rates of genetic response and inbreeding: the number of reference sires used (1, 2 or 3), the number of females per flock mated to reference sires (a total of 10, 15 or 30 females), and the selection intensity for reference sires in the scheme (highest ranking, or from the top sixth or top third available). Genetic progress increased with increasing intensity of selection and use of reference sires. However, these gains can be achieved at acceptable levels of inbreeding because of the larger population size (Lewis and Simm, 2000). SRS rely on good genetic links between flocks for their success. Collaborative research at SAC and the Roslin Institute has produced a method of measuring the strength of genetic links (or connectedness) between existing or potential new members in SRS, in order to identify where reference sires need to be used more widely to allow reliable comparisons across flocks (Lewis *et al.*, 1999). This algorithm is in use in industry SRS in Britain. Work is still underway to precisely define sufficient connectedness.

Over the last 11 years, SRS have been formed in over 20 sheep breeds in Britain, including all of the major specialized meat breeds. About half of performance-recorded flocks in Britain (and about two thirds of performance-recorded sheep) now belong to these schemes. High rates of responses to index selection for lean growth are being achieved (about 1.75% per annum in the specialized meat breeds). These schemes also have the ideal structure to exploit new technologies cost-effectively and thus we anticipate that molecular techniques and new selection criteria (e.g. CT) will rapidly be adopted within such schemes.

CONCLUSIONS

Carcass composition can be changed directly through selection or indirectly by changing the size of animals at maturity. A joint strategy is commonly used, although increases in live weight must fit within the context of overall efficiency of meat production. Increasing carcass leanness is central to most small ruminant breeding programs for meat, although muscle shape, eating quality and concerns over food safety and production methods need to be considered in the goal. Live weight and ultrasound fat and muscle depth are the criteria often combined in indices to affect carcass composition, and substantial improvements have been achieved in experimental flocks and industry by their use. X-ray CT in two-stage selection schemes offers opportunity to accelerate gains further, particularly within cooperative breeding programs designed to overcome structural constraints in small ruminant industries.

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