INTRODUCTION

A basic principle of animal production is that individual performance is determined by genetic makeup and environmental conditions. Accordingly, individuals with above average phenotypes can result from superior genotypes, favourable environments, or both. Prior to weaning, it is the prenatal and then milking and mothering ability of the dam that provides an important component of a young animal's environment. Although the milking and mothering ability of the dam is an environmental effect from the viewpoint of the young animal, it is affected by the genotype of the dam for milking and mothering ability. Thus, weaning weight is determined by individual genotype for preweaning growth (direct effect D), genotype of the dam for milking and mothering ability (maternal effect M) and effects of the environment (E).

Weaning weights of beef cattle can be modified by genetically increasing preweaning growth ability of calves, using dams with superior maternal ability, or by providing a better environment through improved management practices. Maternal effects can be a major determinant of performance up until weaning, but thereafter tend to diminish in importance with age as postweaning genetic and environmental factors dilute their effect.

Using crossbreeding, farmers can make use of breed differences in both growth rate and maternal ability. In a trial involving 9 crossbred dam breeds and purebred Angus cows, Carter and Muller (1977) demonstrated that, relative to purebred cows, total productivity index (based on 2 yr reproductive success and weight of calf weaned) was almost 50% greater with Jersey-Angus and Friesian-Angus crossbred cows. Crossbred cows with good maternal ability can be mated to a sire breed with large mature size (e.g. Charolais, Simmental), to produce calves with superior growth potential which are nurtured by cows with good maternal ability.

The objective of this paper is to describe characteristics of within breed selection for traits with maternal influence, such as weaning weight in beef cattle. There are several factors which complicate improvement programmes for traits with maternal influence (Willham 1963, 1980). First, there may be a negative genetic correlation between direct and maternal effects. Second, the dam contributes both the maternal effect and half of the direct genes, leading to difficulties in accurately separating direct and maternal contributions. Third, the expression of maternal effects are sex limited and occur late in life, a generation behind the direct effects. Finally, there is evidence of a negative environmental covariance between generations such that a heifer calf whose dam had good maternal ability may carry genes for good maternal ability but have inferior performance.
Studies on beef cattle weights have reported substantial genetic variation within breed in both direct and maternal effects. In many cases, the estimated genetic correlation between direct and maternal effects has been moderate and negative, -0.3 to -0.4. (e.g. Hohenboken and Brinks 1971; Garrick et al 1989). A negative genetic correlation indicates a tendency for animals with superior growth genes to have inferior maternal genes and animals with inferior growth genes to have superior maternal genes. This would suggest that genes which partition nutrients to increase body reserves (growth of a young calf) are partly incompatible with genes which partition nutrients away from the body to the mammary glands of a lactating cow. A negative genetic correlation may be the result of many generations of natural selection with an intermediate optimum.

Traits with moderate heritability (such as fleece weight) can be effectively improved by mass selection, whereby parents of the next generation are chosen on the basis of superior phenotypes. Mass selection on traits with a negative genetic correlation between maternal and direct genetic influence can be used to increase either the direct or maternal component to the detriment of the other (Van Vleck 1970). Both components would increase if the genetic correlation is positive.

One approach for concurrent genetic improvement of two traits with a negative genetic correlation is to form separate lines. A sire line would be bred to improve the direct genetic growth and a dam line selected for maternal ability. Wherever possible, slaughter progeny would be obtained by crossing these lines. Such a mating plan is already widely used with sire lines and dam lines representing different breeds.

A correlation of -0.3 to -0.4, indicates that calves with above average genetic merit for direct growth will tend to be genetically below average for maternal ability. The association is not perfect so that a group of animals with similar direct genetic effects will have a range of maternal genetic effects. Although not common, outliers with superior direct and maternal genetic effects will exist. For example, the American Simmental Association 1988 National Sire Summary lists 50 bulls which are proven trait leaders (in top 10% active bulls) for maternal ability and six of these bulls are also trait leaders for direct growth. These highly desirable animals may be hard to identify without progeny testing.

CONFOUNDING OF DIRECT AND MATERNAL CONTRIBUTION OF DAM

Crossfostering trials have been used to separate the genetic and postnatal environmental contributions of the dam. Embryo transfer trials can be used to some extent to separate genetic from pre- and postnatal and environmental conditions. Statistical analyses of experimental (e.g. Hohenboken and Brinks 1971) and field data (e.g. Garrick et al 1989) have provided estimates of relative contributions of direct and maternal effects. These variance component estimates are a prerequisite for genetic evaluations which can predict direct and maternal breeding values of individuals.

Mass selection based on weaning weight is not suitable for customised improvement of direct and maternal genetic effects. Information on relatives is essential to accurately separate direct and maternal contributions. This requires individual animal identification, recording of parentage at mating (through artificial insemination or single-sire mating groups) and relating offspring to dams at calving, in addition to recording of individual weaning weights.
Given estimates of variance components and weaning weight records on individual calves and their relatives, a statistical analysis is required to predict genetic merit. One approach is to describe weaning weights using a model which includes sires (contributing half the direct effect) and maternal grandsires (contributing one-quarter direct effect and one-half maternal effect). Bulls can be evaluated as sires (S) and as maternal grandsires (MGS), enabling an estimate of the maternal contribution (MGS - 0.5S). The evaluation of maternal effects using all relatives' records has been greatly facilitated by the discovery of an algorithm which enables all relatives to be included in an analysis (Henderson 1976).

Commonly used breeding values for maternally influenced traits are maternal grandsire effect (0.25 direct plus 0.5 maternal) or dam effect (maternal plus 0.5 direct) (Ponzoni 1988; Nicol et al 1985). These weightings reflect the confounding of direct and maternal effects in maternal grandsires and dams but are not necessarily appropriate weightings for selection programmes.

**TIME OF EXPRESSION OF DIRECT AND MATERNAL EFFECTS**

The expression of maternal effects are sex limited and occur late in life, after replacements have been selected and allowed to reproduce. This leads to difficulties in assessing maternal effects free of the effects of culling on direct effects and requires sophisticated techniques for genetic evaluation. Prior to selection decisions being made on male and female replacements, estimates of maternal genetic effects will rely on ancestor evaluations.

Suppose selection is for the direct component and the genetic correlation between direct and maternal effects is negative. Selection for the direct component will allow the direct component to increase in one generation, but a generation later that gain is offset by a decrease in the maternal component (Van Vleck et al 1977). Accordingly, within breed selection is best practised on an index which combines direct and maternal genetic effects with appropriate relative economic values. These values may depend on whether producers market offspring at weaning, yearling or older ages.

In the short term, the value of a calf marketed at weaning may not be influenced by the relative contribution of direct vs maternal influence. However, sires produce offspring which are slaughtered as well as used as replacements, with a greater time lag for realising benefits of superior maternal genotypes than benefits of superior direct genotype. Appropriate economic weightings for direct and maternal contributions should account for the frequency of expression of direct and maternal genotypes and discount for time of expression. Ponzoni (1988) cites an example which suggests relative weightings of 1.25:1 for direct:maternal effects. Further research in selection objectives for beef cattle is required.

**INTERACTIONS BETWEEN GENERATIONS**

There is some evidence that correlations between offspring and dam weaning weights are not as high as expected from knowledge of direct and maternal variation (Mangus and Brinks 1971; Hohenboken and Brinks 1971; Van Vleck et al 1977). One explanation is that a negative environmental covariance exists between generations such that a heifer calf whose dam had good maternal ability may carry genes for good maternal ability but have inferior performance. A biological justification for this finding is that excess adipose tissue may be laid down in the mammary gland when heifer calves grow too fast prior to weaning, impinging on their own future lactational performance (Johnsson and Obst 1984).
Estimation of the environmental covariance between daughters and dams has had little recent attention. It is ignored in genetic evaluations of beef cattle. The existence of a negative environmental covariance would likely impact cow selection rather more than sire selection. This area is worthy of further research.

SUMMARY

Maternal effects can be an important component of variation within breeds as well as between breeds. Maternal influence on economic traits measured early in life justifies their inclusion in selection objectives for beef cattle. Unfavourable relationships between selection for direct growth and increased cow size may further favour selection for maternal components. A detailed study of selection objectives for beef cattle is warranted.

Genetic and environmental relationships between direct and maternal influences complicates the inclusion of maternal effects in selection programmes. More sophisticated on-farm recording and data processing are required for genetic evaluations with maternal effects than for traits controlled solely by genes with a direct influence.

REFERENCES


