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Selection for Reproductive Efficiency

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Number of lambs weaned per breeding ewe has a greater influence on productivity of the sheep enterprise than any other trait. Net reproductive rate is determined by several components, with fertility, prolificacy (litter size) and lamb livability having the greatest influence (Wang and Dickerson, 1991). Age at puberty, prenatal viability and, in some enterprises, out-of-season fertility, can also contribute.

Fertility and lamb viability.

Fertility does not usually receive direct emphasis in selection programs, since it is obviously subject to continuous natural selection, and reported heritability estimates average less than 0.10 (Fogarty, 1995). However, heritability estimates are on average positive, and the importance of the trait indicates it merits attention, at least in flocks/environments where mean performance is low (less than 90%). Ewes dry in any year can be culled, or, if the cost of replacements and history of subsequent performance of such ewes in the flock indicates they should be kept for economic reasons, it is recommended they not be included in the group producing replacements in future years. Since most genetic change in sheep flocks results from sire selection, rams should be consistently selected from dams that have lambed every year. The National Sheep Improvement Program (NSIP) can provide genetic evaluations for fertility if producers do a good job of recording all breeding opportunities, deaths, disposals, etc. on the NSIP data input sheets. However, at present not all producers do so.

Lamb survival is also a trait for which heritability estimates average less than 0.10 (Fogarty, 1995; Matos et al. 2000; Morris et al. 2000). Also, as for fertility, survival data are often not well recorded; lambs that do not survive as well as ewes that do not lamb may not be included. However, as emphasized by Shelton and Willingham (this issue), reducing lamb mortality offers one of the best opportunities to increase flock productivity. Selection for improved lamb survival may be a means of contributing to that goal. The reports by Matos et al. (2000) and Morris et al. (2000) indicate that maternal genetic effects may be as large as or larger than direct genetic effects on this trait, and that additive direct and additive maternal effects are positively correlated. Thus selection programs that utilize both direct and maternal variance may lead to significantly more response than indicated by direct heritability only, reinforcing the value of complete recording and genetic analyses.

The existence of useful genetic variation in fertility and lamb livability is also indicated by differences among breeds (Cundiff et al., 1982; Fogarty et al., 1984b) and among selected lines (Bradford et al., 1999) in these traits. Where use of different breeds or lines is feasible, such information may be used to improve genetic potential.

Litter Size.

Of the three most important components of reproduction, the one with the greatest potential for change by selection is litter size, i. e. number of lambs born per ewe lambing. There is also much variation between breeds; breeds are available with mean litter size ranging from slightly above 1.0 to above 3.0 (Leymaster, this issue). There are many reports, for example by Dickerson (1977), Hulet, (1984), Snowder (2001) documenting the use of breed variation in the development of composite populations with higher mean litter size than traditional US breeds. A case history documenting use of such variation to increase productivity of a commercial flock is reported elsewhere in this issue (Hamilton and Hamilton). Where market demand and environmental conditions permit use of some prolific breed inheritance, litter size can be increased substantially in one generation, i. e. much more rapidly than by selection. However, there are situations where selection within a breed will be the approach of choice.

Within breeds, typical heritability estimates for this trait are quite low, of the order of 10% or less (Fogarty, 1995; Notter, 1998; Bromley et al., 2000; Lee et al., 2000). However, the coefficient of variation is high, about 35% (Sakul et al., 1999; Rao and Notter, 2000), compared to 13-15% for adjusted weaning weight (Sakul et al., 1999). This permits quite large selection differentials for litter size, and there are several reports of substantial change effected by within flock selection. The earliest well-documented reports were those by Turner et al. (1962), and Wallace (1964). Bradford (1985) reviewed the results of those and several other selection trials, and concluded that an annual increase of 1-2% in average litter size could be achieved by selection. Responses to selection for litter size or twinning rate reported by Burfening et al. (1993) and Saboulard et al. (1995) in western US range sheep were also within this range.

The conclusion of 1-2% per year was based on experiments carried out before the availability of the animal model for genetic evaluations. This statistical method permits systematic use of information on all recorded relatives, which can significantly increase rate of response to selection. While no actual selection experiments to measure the amount of increase in rate of response for litter size have been reported to date, it seems probable that a rate of 2%/yr, the high end of the range listed, and possibly more, could be achieved. Utilization of this potential will depend on parentage identification of all animals, recording of numbers of lambs born in all lambings, genetic evaluations from the resulting data, and use of the results in selection decisions, particularly in sire selection.

The annual gains listed may seem small, but an increase of 20%, suggested as possible over a 10-year period, may represent as much increase as desired. There is also the possibility of "jump starting" the process by an initial screening of exceptionally prolific ewes from a larger population to establish the foundation flock. Several of the experiments evaluating the effects of selection for litter size have involved selection of the most prolific ewes from a larger population to initiate the improvement program. The initial screening generally produced a substantial difference, as much as 10% of the base flock mean, in the first generation progeny (Wallace, 1964; Turner, 1978; Hanrahan, 1982; Sakul et al., 1999). Subsequent response varied, from slow response for more than 10 generations (Sakul et al., 1999), to little response for some time and then a rapid response (Clarke, 1972), to continuous good response (Hanrahan, 1982). Although there have not been enough experiments for firm generalizations, it appears that initial screening, where feasible, is an effective means of producing an immediate increase in genetic potential for litter size, and that this does not preclude subsequent response to selection within the screened group.

The heritability of 0.10 for litter size mentioned above relates to individual records, i.e. to the response expected form selection based on one record per ewe. The heritability of the average of two or more records will be higher. If single record heritability is 0.10, that for the mean of 2, 3, 4 and 5 records is expected to be approximately 0.18, 0.24, 0.29 and 0.33, respectively, suggesting use of lifetime prolificacy as a means of increasing selection response. Supporting this conclusion, Shelton and Menzies (1968) reported heritability estimates above 0.20 for mean numbers of lambs born and weaned, based on records from all years the ewes were in the flock. Generation interval may be longer if selection decisions are deferred until additional records are available. However, ewes normally stay in the flock for several years in any case, and all available records should be used. The problem of longer generation interval can be minimized by selecting rams from dams with several records but turning ram generations rapidly, for example by using ram lambs where that is feasible, and using rams in seedstock flocks only one year.

Okut et al. (1999) present evidence that heritability of litter size differs with ewe age, and that genetic correlations vary between records at different ages. They suggest that accuracy of selection could be increased by considering age of ewe as part of the trait, rather than simply adjusting for ewe age.

Ovulation rate is the most important factor affecting litter size, and it has been suggested that selection on ovulation rate would be an effective means of increasing the rate of genetic change in litter size (Hanrahan, 1974, 1982; Hanrahan and Quirke, 1985). Waldron and Thomas (1992) estimated that adding information on ovulation rate would increase rate of genetic change in litter size by 23% compared to use of litter size data only. An experienced operator can measure ovulation rate rapidly and accurately by means of laparoscopy, and this trait has the advantage of permitting repeated measurements within a season. It is a potentially useful aid to selection, but the extra cost of obtaining the information may be justified only in breeding flocks with an effective marketing program for improved breeding stock.

Scrotal circumference has also been suggested as an aid to selection for litter size (Waldron and Thomas, 1992; Burfening and Davis, 1998). However, as these reports indicate, the genetic relationship with litter size is quite low, and an apparent negative genetic association between testis size and body weight (Land, 1982; Burfening and Davis, 1998) raise doubts about the value of including information on this trait in a selection program to improve litter size.

It is often assumed that the ewe determines the number of lambs born, and that the ram (once the eggs are fertilized), and the genotype of the embryo, have little or no influence. A number of reports support that conclusion (Bradford, 1972; Hanrahan, 1982; Hanrahan and Quirke, 1985; Burfening and Davis, 1996). However, results of some trials indicate significant effects of the genotype of the male and/or embryo on litter size. Compelling evidence comes from differences in litter size of ewes with two ovulations mated to rams of different breeds (Meyer, this issue). Vakil et al. (1968) reported significantly larger litter size for ewes of the same birth type when mated to twin-born than to single-born rams. Burfening et al. (1977) reported significantly more embryos from use of rams from a high- than from a low-prolificacy line, when both were mated to unrelated ewes. Clearly, genotype of the sire or embryo can contribute to variation in litter size, and it may be possible in programs such as NSIP to obtain estimated breeding values that utilize this variation.

Regardless of the strategy followed to increase litter size, it is important to keep in mind that the optimum is not necessarily the maximum achievable. A target mean value appropriate to the particular management system, feed resources and lambing season for the flock(s) in question should be set before a selection (or crossing) program is initiated.

Optimum litter size at birth is influenced by survival rates of singles, twins and higher multiples, and by the growth rate of survivors. Bradford et al. (1991) summarized results from several studies that gave average numbers of lambs weaned of 0.89, 1.63 and 1.63 for litter sizes of 1, 2 and 3 at birth, although it must be emphasized that survival rate varies widely between flocks, especially for triplets. The advantage in total weight of lamb weaned for twin compared to single births is generally very large, even with the lower individual weaning weight of twins. Thus twin births will nearly always be preferable to single births, at least for mature ewes. However, based on the above mean survival rates, there would be no advantage for triplets compared to twins, and possibly some disadvantage, considering the more variable and, on average, lower weaning weight of triplet born than twin born lambs.

Survival rates for triplet lambs can be increased, in some cases substantially, with improved management at lambing and a good lamb fostering program, improving the relative performance of ewes bearing triplets. Also, there are flocks where the milk production potential, nutrition and management are such that a higher percentage of ewes can raise triplets successfully, which would also improve the relative value of triplet births. However, in the majority of US sheep operations, at least at present, two may be the maximum number of lambs that ewes can raise satisfactorily. In this situation, the optimum mean litter size is likely to be that which results in no more triplets than those from which the third lamb can be successfully grafted to ewes with singles or that have lost lambs. Thus a mean of, say, 1.85 born (25, 65 and 10% of ewes with 1, 2 and 3, respectively) might be the maximum acceptable. A flock with less variation, e. g. 15, 80 and 5 % 1's, 2's and 3's (mean 1.90) would be preferable, but variation due to ewe age, nutrition and unknown environmental factors as well as genetic differences among ewes usually results in greater variation than this.

There may also be management situations where twinning is desirable but with essentially zero tolerance for triplets. In such flocks the optimum mean may be of the order of 1.6 (40% singles, 60% twins), since most flocks with a twinning rate above 60% will have at least a few triplets.

The above refers to target mean litter sizes for ewes 2 years and over at lambing. Both the optimum and actual mean for yearling ewes will be lower.

It is also important to note that season of lambing and prebreeding nutrition each has a substantial influence on litter size. Ewes of the same genetic potential lambing in fall will have significantly lower litter size than the same ewes, in the same condition, lambing in late winter or spring. Shelton and Morrow (1965) reported litter sizes of 1.27, 1.26, 1.50 and 1.55 for comparable groups of Rambouillet ewes lambing in August, November, February and May, respectively. Fogarty et al., 1984a; Sakul et al. (1999) and Notter (2000) also reported large differences in litter size at different seasons. Body condition and nutrition level prior to and at the time of mating can also affect mean litter size to at least a comparable extent. Thus in setting a target litter size, or assessing whether a particular breed or cross will meet a defined target, the information used should come from the season and under the nutrition and management conditions in which the ewes will be expected to perform.

Age at puberty.

In annual lambing systems, ewes may be bred to lamb first at either one year (12-15 mo.) or at two years of age. The primary factor affecting choice is usually feed supply – are the ewes well enough grown out to have good fertility at 7-10 months, and is nutrition during pregnancy and lactation adequate for satisfactory survival and growth of their lambs? Another consideration is whether an extended lambing season is compatible with feed, management and markets; performance at 14-15 months tends to be much better than at 12 months. Notter (2000) reported that 15-month old ewes averaged 0.21 more lambs born than 12-month old ewes. However, the 15-month age means lambing these ewes 3 months later than the older ewes in the flock. Where the latter works, it can represent a very productive system (Hamilton and Hamilton, this issue).

In a number of production systems in the US, lambing ewes at one year of age is not feasible, and in this case age at puberty is not a consideration. However, if the average ewe leaves the flock at 5.5 years of age, she will have four years production if she lambs first at two years, and five years if she lambs as a yearling. Assuming first year lamb production is 60% of the average at later ages, lifetime lamb production will be 15% higher (4.6/4.0) for ewes lambing as yearlings. This represents potentially a significant advantage in net income of the operation, although the extra feed and labor for the yearling ewes may result in a net improvement somewhat less than 15%.

Where successful breeding of ewe lambs is compatible with the management system of the flock, early puberty is an essential attribute. A conception rate of 80% or better is suggested as a target if first year breeding is to justify the extra investment in feed and labor required, particularly in larger flocks where this group is likely to be a separate management unit. Most "farm flock" breeds under the feed conditions of that production system will have good fertility as ewe lambs. However, range breeds such as the Rambouillet tend to have later puberty (Dickerson and Laster, 1975; Quirke et al., 1985) and thus lower fertility their first year, even under relatively good conditions.

The estimated heritability of age at puberty is about .25 (SID, 1997), and improvement will almost certainly result from selection. If some but not all ewe lambs will breed and lamb as yearlings, several generations of selecting rams and ewes from dams that have lambed as yearlings should produce a steady increase in first year performance.

An alternative approach is to introduce some inheritance from an early puberty breed. The Finnsheep and Romanov breeds consistently show very early puberty. Crossbreds or composites that have 25% (or more) of their inheritance from one of these breeds have been shown to have very good fertility as ewe lambs in any environment which will adequately support first year lambing. Thus use of a 50% Finnsheep or Romanov ram on ewes of a later puberty breed can produce, in one generation, a marked improvement in first year breeding performance. The many years saved compared to within breed selection in achieving consistent first year breeding performance could compensate for the somewhat lower performance in fleece and carcass traits typical of crosses of these two early puberty breeds. These breeds also contribute increased prolificacy, and selection can improve fleece and carcass traits if these are important to the operation.

Genetic variation in prenatal survival (Meyer) and selection for out-of-season breeding (Notter) are considered elsewhere in this issue. A practical means of selecting for out-of-season fertility is to use the rams intended as sires of replacement ewes (or ewes and rams) only for the first few weeks of the breeding season, and to use other rams, e. g. terminal sire breed rams, for the remainder of the season. In this way, all replacements will come from early lambing ewes. (The practice, occasionally observed in some flocks, of using whiteface rams at the end of the season to produce replacements will select against early season fertility).

Much of the research related to genetic parameter estimation and selection for reproductive rate has focussed on components of reproduction – litter size, fertility, etc. Selection for traits such as litter size does increase flock productivity, for example total weight of lamb weaned per ewe, as shown by the results of several of the experiments cited in this review. However, the results from the US Sheep Research Station at Dubois reported by Ercanbrack and Knight (1998) and Snowder (this issue) make a strong case that selecting directly for total weight of lamb weaned per ewe will lead to more improvement. The selection responses reported by those authors were surprisingly large. Other long term evaluations of direct selection for total litter weight have not been reported, but typical results of selection for performance traits in sheep suggest that response may be less than realized in those experiments. Nevertheless, total litter weight weaned represents a "biological index" which incorporates variation in fertility, litter size, viability, and growth rate, and no doubt other components not normally recorded. Selecting directly for it should in fact result in more improvement than selecting for components. No extra recording is required, since information on total litter weight will be available if its principal components, numbers of lambs weaned and weaning weights, are recorded. It is therefore recommended as a practical and useful selection criterion to improve flock productivity.

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