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*J Anim Sci* 1997. 75:2033-2040.

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# Response to Selection for Fertility in a Fall-Lambing Sheep Flock

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**ABSTRACT:** Selection for fertility in a fall lambing system was applied for 5 yr (1.45 generations) in a crossbred sheep population. Three flocks were involved: a fall-lambing selected (S) flock of 125 ewes and 10 rams, a fall-lambing environmental control (EC) flock of 55 ewes and five rams, and a spring-lambing genetic control flock of 45 ewes and five rams used to produce replacements for EC. Estimated breeding values for fertility (ewes lambing per ewe exposed) were calculated for animals mated in each year of the study using a single-trait animal model and increased more rapidly in S (.0138/yr) than in EC (.0067/yr). After accounting for genetic drift, EBV of ewes mated in S in the final year of the study averaged  $.070 \pm .032$  ( $P = .08$ ). A correlated response of .0087 lambs/yr was observed in S for fall litter size. Genetic trends in all body weights were positive in EC, likely because of supplemental selection on body size in ram lambs used in EC. Ninety-day weight,

maternal effects on weaning weight, and 90-d scrotal circumference increased in S, but direct effects on birth and weaning weights declined. In order to focus on realized selection response in fertility, EBV for fertility of 330 replacement ewe lambs from S and EC were calculated using only data collected after their birth. These realized EBV were then regressed on pedigree EBV calculated at the time the ewe lambs were born. The regression was significant when all relationships were used to calculate both EBV ( $.20 \pm .08$ ) but only approached significance ( $.13 \pm .07$ ) when only records of the ewe lambs themselves, their descendants, and their paternal half-sibs were used to calculate realized EBV. Also, EBV for all ewes were calculated at the start of each breeding season and were higher ( $P < .01$ ) for ewes that subsequently lambed than for open ewes. These results suggest that selection can be used to improve fertility in fall-lambing sheep flocks.

Key Words: Sheep, Reproduction, Fertility, Selection, Genetic Trend

J. Anim. Sci. 1997. 75:2033–2040

## Introduction

Seasonality of breeding is a major impediment to improvement of reproductive efficiency in sheep. Results of previous attempts to develop sheep populations with an extended breeding season have been equivocal because of inadequate control populations and/or failure of apparent accumulated genetic superiority to be expressed in other environments (Thrift et al., 1971; Lindahl and Terrill, 1975; Jenkins and Ford, 1982). Documentation of realized selection response is also often complicated by the low heritabilities of fertility traits (Fogarty, 1995) and by the

large population sizes that are therefore required. However, mixed-model methodology with animal models can be used to provide relatively efficient estimates of selection response (Blair and Pollak, 1984; Parnell et al., 1986; Southwood and Kennedy, 1991; Cantet et al., 1993). The use of mixed models allows separation of genetic and environmental effects and takes into account relationships among animals as well as effects of cumulative selection and nonrandom mating, provided all information related to the selection is included in the analysis (Henderson, 1975; Sorensen and Kennedy, 1986; Kennedy, 1990).

The objective of this study was to estimate genetic and environmental trends for spring fertility and fall litter size as well as genetic changes in birth, weaning, and 90-d weights and 90-d scrotal circumference in a composite sheep population under selection for ability to lamb in the fall.

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Received August 19, 1996.

Accepted April 11, 1997.

## Materials and Methods

Establishment of an experimental flock containing 50% Dorset, 25% Rambouillet, and 25% Finnsheep breeding began in 1983 (Fossceco and Notter, 1995). The flock was maintained under an annual spring lambing system until the spring of 1987, when the population was divided into a selection line (**S**) and two control lines. The S flock of 125 ewes and the environmental control (**EC**) flock of 55 ewes were transferred to an annual fall-lambing system and were mated in that system for the first time in spring 1988. The genetic control (**GC**) flock of 45 ewes remained in the annual spring lambing system and was used as a source of unselected replacement animals for the EC flock (Al-Shorepy and Notter, 1996). Two control flocks were required because progeny of fall-lambing EC ewes would automatically be selected for ewe fertility in spring and would therefore be inappropriate replacements for a control line. A result of this experimental design was a constant 7-mo age difference between S and EC ewes.

In the S flock, up to one-third of the ewes (42 ewes) were replaced each year, depending on the number of available ewe lambs. Ewes were removed from S as necessary for physical unsoundness (primarily mastitis), with additional ewes culled based on mean fertility. However, no ewe was culled based on performance until after her second opportunity to lamb because of the very low fertility of ewe lambs. Available ewe lambs were ranked based on the mean fall fertility of their dams, with the best 42 identified as replacements. All ewe lambs were then exposed to rams in the spring at 7 to 8 mo of age, and any ewe lamb that became pregnant was retained. Following pregnancy diagnosis in midsummer or after fall lambing, open ewe lambs not included in the original group of 42 were culled. Thus, all pregnant ewe lambs in S were kept as replacements, with additional open ewe lambs retained (up to a total of 42) based on mean fertility of the dam.

Ten rams were used in S each year. Four to seven of the rams were replaced each spring with 7- to 8-mo-old ram lambs born in the previous fall. The target number of ram lambs to be used in each year was originally set at five but increased during the course of the study because their fertility in spring matings was found to be equal to that of older rams. However, in 1989 only four acceptable ram lambs were identified. Ram lambs used in S were initially chosen based on the mean fertility of their dams. Candidate ram lambs then underwent a breeding soundness examination. Those that passed the breeding soundness examination also underwent a semen evaluation and a libido test. These tests were used only to screen out ram lambs that were questionable breeders, not to provide additional information for ranking of candidate replacement ram lambs. Requirements for body

weight and scrotal circumference (**SC**) in the breeding soundness examination generally dictated that replacement ram lambs must come from the top one-half of available ram lambs in weight and SC. The libido test involved exposure of ram lambs to one to three estrous ewes for a period of 5 to 20 min. Ram lambs that completed several (generally three or more) matings in that period were considered acceptable. Ram lambs that did not mate were generally separated from ram lambs that had passed the test, penned overnight with estrous ewes, separated from the ewes the next morning, and reevaluated the next afternoon. Ram lambs were excluded following semen evaluation if motile spermatozoa were not present in a semen sample obtained by electroejaculation. Ram lambs that did not provide motile spermatozoa were usually not culled until they were reevaluated 1 to 3 d later. Specific numbers of ram lambs excluded from consideration based on semen and(or) libido evaluation were not recorded but were approximately 25 to 35% of candidate ram lambs. No more than two ram lambs from the same sire were used in S in any year.

Older rams in S were culled primarily on their own fertility in their first year of use. Each ram was exposed to approximately 13 ewes and ewe lambs. Older rams were also subject to the same breeding soundness, semen, and libido evaluations used for ram lambs. Rams in S were normally used for at most 2 yr; only two of 37 rams were used for a third year.

In the EC flock, ewes were culled at random within a year of birth, and the proportion of EC ewes from each birth year was adjusted annually to approximately match that in S. Replacement ewe lambs for EC were chosen at random from GC ewe lambs born in the previous spring, but with the restriction that ewe lambs from litters containing two or more ewe lambs be divided at random between GC and EC. Rams used in EC were chosen at random from GC but were subject to breeding soundness, semen, and libido evaluations and therefore usually came from the top one-half of available GC lambs in weight and SC. Five rams per year were used in EC. Each was mated to approximately 11 ewes per year. The proportion of new rams used in EC was approximately the same as in S. No more than one ram lamb per sire per year from GC was used in EC.

The spring-lambing GC flock contained 45 ewes. Because S and GC ewes were not directly compared, culling rates in GC were minimized to reduce genetic drift. Ewes were culled only for obvious unsoundness or if they failed to reproduce for two consecutive years. Replacement ewe lambs for GC were chosen at random as needed, with an average of 7.5 ewe lambs retained per year. Replacement requirements of GC and EC required use of essentially all GC ewe lambs. Sire families were identified in GC when the experiment began in 1987. Two representatives of each family were maintained, and when a ram was culled

or died, a son of that sire or of his remaining family member was retained, if possible, as a replacement. Of the 14 sire families present in fall 1987, 12 were still represented in 1993. Five rams per year were used in GC each year and were chosen rotationally from available sire families. Two rams were usually retained for use in GC in adjacent years to provide genetic connections between years. Rams were culled from GC only because of death or physical unsoundness.

Ewes in S and EC were exposed each year for 60 d beginning May 1 and were reexposed for clean-up matings for 30 d beginning about August 1. The GC ewes were exposed for 42 d beginning October 1. Lambs were weaned at approximately 60 d. Details of breeding and management procedures were given by Al-Shorepy and Notter (1996). Traits considered in the present study were fertility for fall lambing, coded as 1 or 0 for ewes that did, or did not, lamb in fall, respectively; litter size per ewe lambing; lamb weight at birth, weaning (60 d), and 90 d; and lamb SC at 90 d. Data for this study came only from fall-lambing S and EC ewes.

For each animal in S and EC, a generation code ( $g$ ) was calculated as  $g = 1/2(g_S + g_D) + 1$ , where  $g_S$  and  $g_D$  are generation codes of sire and dam. Generation codes of foundation animals were set to zero. These generation codes measure the cumulative number of generations separating an individual animal from the base population.

Variance components were estimated and breeding values were predicted simultaneously using single-trait animal models in MTDFREML (Boldman et al., 1993) for data collected from fall 1988 through fall 1993 lambings. For fertility, the model included fixed effects of ewe age and year and random additive animal, permanent environmental animal, and service sire  $\times$  year (i.e., breeding pasture) effects. For litter size, the model was the same, except that service sire effects were not fitted. For birth, 60-, and 90-d weight and 90-d SC, models included random additive direct and maternal effects and permanent environmental effects of the dam. Definitions of fixed contemporary groupings for weights and SC, adjustments for other fixed effects, estimates of variance components, and discussion of alternative models were described by Al-Shorepy and Notter (1996).

Estimates of additive genetic trends in fall fertility and of correlated responses in other traits were derived from EBV of animals in S and EC (Blair and Pollak, 1984; Southwood and Kennedy, 1991). The EBV for animals born before formation of the S and EC lines were averaged and assumed to equal the mean breeding value in the unselected base population. Mean EBV of S and EC animals in subsequent years were then calculated and regressed on year of the study, and the resulting regression coefficients were compared between S and EC.

Estimates of genetic merit within a population at a given time are usually obtained as the mean EBV of animals born in that year. However, for fertility, this definition is not appropriate because the progeny that are born are already a selected sample, representing only the ewes that conceived. For this reason, mean EBV for fertility in S and EC were calculated in three ways: 1) as the average EBV of all lambs born to S and EC parents in each fall; 2) as the average EBV of all ewes mated in S and EC each spring; and 3) as the average of each ewe-ram pair joined in S and EC each spring. Means based on lambs born will show effects of mean annual fertility and will be higher when mean fertility is low, and vice versa. They will also give greater weight to matings that produce larger litters. Means based on ewes mated should be, on average, lower than those for mated pairs in S because the more highly selected sires are not included, but with random mating, estimates of genetic trend should not differ substantially for ewes mated and for mated pairs.

Permanent environmental trends were calculated as averages of predictions of permanent environmental effects for all ewes mated in S or EC in a given year (Cantet et al., 1993). Likewise, service sire effects were averaged over sires used in S and EC in each year and regressed on years to estimate service sire trends.

Trends in EBV over time measure selection that was applied (in terms of selection differentials of animals chosen as replacements) and selection that was realized (in terms of future performance of those replacements). If genetic parameters are known without error and if the model is correctly specified, resulting EBV provide the best available estimate of animals' genetic merit. However, if parameters are in error or if the model is not correct, selection response may not reflect calculated selection differentials. The relative contribution of applied vs realized selection to the estimate of genetic trend will depend on the relative importance of data from ancestors vs the animal and its progeny in calculation of the EBV but will be larger in experiments of short duration than in experiments continued over many years.

To more directly investigate realized selection response, several supplemental analyses were conducted. All were based on attempts to separate information used for selection from information used to evaluate selection response. To achieve this, several distinct sets of EBV were generated. First, for each ewe lamb exposed in the study, pedigree EBV for fertility were calculated using only data accumulated through the lambing season that produced the lamb. Then, EBV for each ewe lamb born in each year were recalculated using only data accumulated after the birth of the lambs. These later EBV were calculated using either all known pedigree relationships or restricting the base population to the current lamb

Table 1. Means for mature ewes (3 yr old and older) for fertility and year constants from the mixed-model analysis for combined S and EC flocks

Year	Mature ewe fertility	Year constant
1988	.33	.085
1989	.68	.403
1990	.60	.345
1991	.53	.253
1992	.46	.242
1993	.76	.450

crop and their sires. The former approach allows future performance of dams and other older relatives of the current lamb crop to contribute to the lambs' EBV, whereas the latter approach allows only relationships to paternal half-sibs and future progeny to contribute to evaluation of the current lamb crop. Put another way, the former approach allows animals that contributed to the selection differentials to also contribute to evaluation of selection response through their future records, whereas the latter approach involves only animals that did not contribute to the observed selection differentials.

Table 2. Genetic trends for all traits, permanent environmental trends for fertility and litter size, and service sire trends for fertility in S and EC<sup>a</sup>

Component and trait <sup>b</sup>	Annual trend in:	
	S	EC
<b>Genetic</b>		
<b>Fertility</b>		
(Lambs born)	.0065 ± .0034	.0009 ± .0031
(Ewes mated)	.0124 ± .0016*	.0012 ± .0040
(Mated pairs)	.0138 ± .0017*	.0067 ± .0017
<b>Litter size</b>		
(Lambs born)	.0092 ± .0009 <sup>†</sup>	.0022 ± .0036
(Ewes mated)	.0068 ± .0008*	.0024 ± .0011
(Mated pairs)	.0087 ± .0014 <sup>†</sup>	.0011 ± .0039
Birth weight	-.0024 ± .0026	.0095 ± .0058
Weaning weight	-.0014 ± .0030	.0101 ± .0068
Maternal weaning weight	.0102 ± .0032	.0108 ± .0050
90-d weight	.0277 ± .0081	.0453 ± .0211
90-d scrotal circumference	.0316 ± .0039	-.0084 ± .0505
<b>Permanent environmental</b>		
Fertility (ewes mated)	.0013 ± .0008	.0024 ± .0010
Litter size (ewes mated)	.0000 ± .0005	-.0004 ± .0002
<b>Service sire</b>		
Fertility (breeding rams)	-.0030 ± .0072	.0068 ± .0158

<sup>a</sup>Trends were derived by regressing yearly means for EBV, ewe permanent environmental effects, or service sire effects on year of the study.

<sup>b</sup>The individuals whose values were averaged to derive yearly means are shown in parentheses. Birth, weaning, and 90-d weight and 90-d scrotal circumference trends were based on lambs born. Maternal weaning weight trend was based on ewes mated.

\*S and EC differ ( $P < .05$ ).

<sup>†</sup>S and EC differ ( $P < .10$ ).

Also, in each year, EBV for fertility calculated before the current exposure were compared for ewes that either became pregnant or remained nonpregnant. These models fit combined effects of year, service sire (breeding pasture), and ewe age at breeding (with four classes: 7 mo for S replacements, 14 mo for EC replacements, 19 to 26 mo for ewes at their second lambing opportunity, and older ewes) as a contemporary group along with the effect of ewe fertility on previous EBV. The heterogeneity of this effect across ewe age classes was also tested by fitting the ewe age × fertility status interaction.

## Results and Discussion

**Population Structure.** Ewes mated in the final year of the study were an average of 1.45 generations removed from the base population for S and an average of 1.13 generations removed from the base population for EC. For S, 17% of the ewes mated were still foundation ewes, 50% were 1 to 2 generations removed from the foundation, 32% were 2 to 3 generations removed from the foundation, and 1% (one ewe) was 3 or more generations removed from the foundation. For EC, comparable values were 9, 82, 9, and 0%, respectively. Service sires used in S in the final year of the study were an average of 1.7 generations removed from the foundation, with a range of 1.5 to 2.75 generations. The mean age of ewes mated in 1993 was 3.4 yr for S and 4.1 yr for GC (the ewes that produced the EC replacements). The mean age of rams used in 1993 was 1.4 yr for S and 3.0 yr for GC.

**Time Trends in Fertility.** Simple means for fertility of adult (3 yr old and older) ewes and year constants (indicative of annual environmental effects) from the mixed-model solution vector are shown in Table 1 for combined S and EC flocks. A substantial negative environmental effect on fertility was observed in the first year of the study, immediately following the change from spring to fall lambing. However, overall linear trends in mature ewe fertility (.041 ± .036) and in year constants from the mixed-model analysis (.036 ± .030) were not significant for the combined flocks.

Positive genetic trends in fertility were observed in S (Figure 1, Table 2) based on lambs born, ewes mated, and mated pairs. Trends based on ewes mated and mated pairs were similar and larger than that based on lambs born, and the estimated response was more consistent (i.e., the SE was smaller). When genetic trend was based on lambs born, variation in response was increased because of variation among years in mean fertility. This situation was most evident in 1988 (Figure 1), when mean fertility was low. The lambs born represented a highly selected sample, and therefore have relatively high EBV.

Genetic trends in fertility in EC were also positive, and were significant per mated pair, but were less

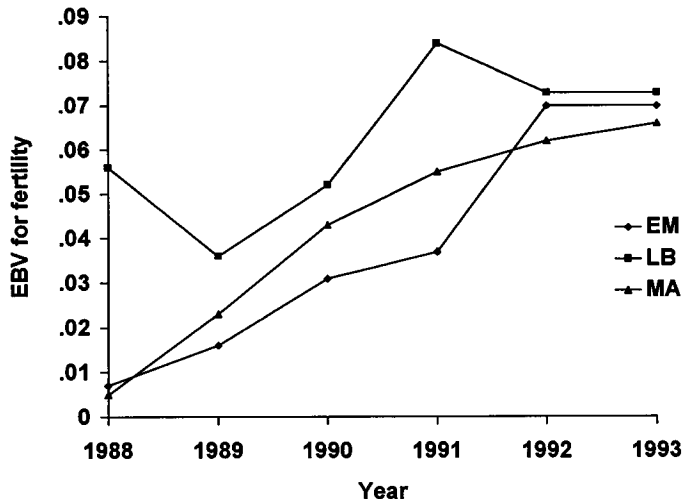


Figure 1. Genetic trends in fertility EBV in the S flock based on mean EBV of lambs born (LB), ewes mated (EM), or mated sire-dam pairs (MA) in each year.

than those in S (Figure 2). Small positive genetic trends in fertility in EC could occur as a correlated response to natural selection for fertility and litter size in GC or as a result of genetic drift.

Estimates of genetic trends in Table 2 do not explicitly account for drift variance (Hill, 1971). The relatively small SE of the regression coefficients reflect this omission as well as the limited range and "smoothing" of the response (Sorenson and Kennedy, 1986) that result when phenotypic deviations are regressed to derive EBV. If selection response is estimated as a linear function of EBV, the variance of the estimator (including drift variance) may be derived as  $\text{Var}(\mathbf{k}'\hat{\mathbf{u}}) = [\bar{a} h^2 - \bar{c}(1 - h^2)]\sigma^2$ , where  $\hat{\mathbf{u}}$  is the vector of EBV,  $\mathbf{k}'$  is the vector of linear weightings that defines the estimator,  $h^2$  is heritability,  $\sigma^2$  is phenotypic variance,  $\bar{a}$  is the average additive relationship among individuals, and  $\bar{c}$  is the average

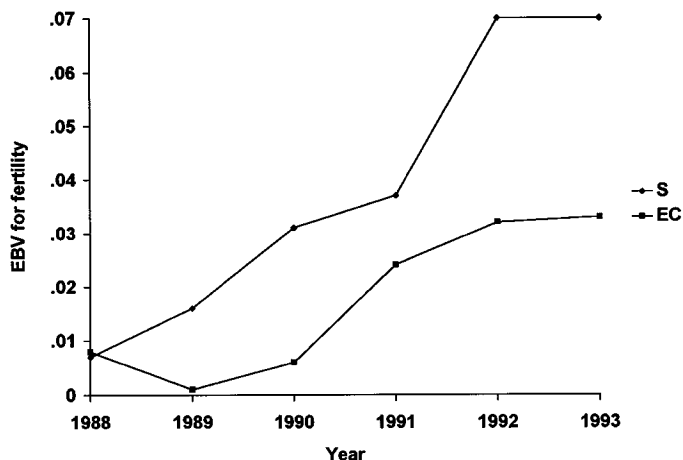


Figure 2. Genetic trends in fertility EBV for ewes mated in S and EC in each year.

element of the prediction error (PE) covariance matrix of  $\hat{\mathbf{u}}$  (Sorenson and Kennedy, 1986; Kennedy, 1990). Exact calculation of  $\text{Var}(\mathbf{k}'\hat{\mathbf{u}})$  is difficult because of the large number of off-diagonal elements of the additive relationship and PE covariance matrices that must be considered, especially for a relatively complex estimator such as the regression of mean EBV on year that uses EBV from essentially all animals born in the project.

An alternative and, from the viewpoint of drift variance, less complicated estimator of selection response is the mean EBV for fertility of all ewes mated in each line in the final year of the study (.070 for S and .033 for EC; Figure 2). Vector  $\mathbf{k}'\hat{\mathbf{u}}$  now involves only ewes mated in 1993. The contribution of genetic drift ( $\bar{a} h^2 \sigma^2$ ) can be approximated as  $2 \bar{F} h^2 \sigma^2$ , where  $\bar{F}$  is the mean inbreeding of progeny of the ewes (Kennedy, 1990). Values of  $\bar{F}$  were .048 for S and .030 for EC. The estimate of  $h^2 \sigma^2$  was .012 (Al-Shorepy and Notter, 1996). Resulting estimates of drift variance were .0015 for S and .00072 for EC.

Prediction error variances for fertility EBV for the 119 S and 55 EC ewes mated in 1993 were obtained from the MTDFREML program and averaged .00927 for S and .00980 for EC, corresponding to mean accuracies of EBV of .47 for S and .42 for EC. Prediction error covariances are not easily obtained from MTDFREML for large numbers of animals. However, linear functions of EBV and associated SE can be obtained, and PE variances of EBV differences  $[V(d_{ij})]$  can be compared to PE variances of component EBV  $[V(\hat{u}_i)]$  to estimate PE covariances ( $c_{ij}$ ) as  $c_{ij} = [V(\hat{u}_i) + V(\hat{u}_j) - V(d_{ij})]/2$ . Values for  $c_{ij}$  were derived for 25 random pairs of S ewes and 10 random pairs of EC ewes, with mean values taken as representative of mean PE covariances for each line. Means for  $c_{ij}$  were .00061 for S and .00093 for EC, corresponding to mean PE correlations for fertility EBV of .07 for S and .09 for EC. When PE variances and covariances were weighted and summed, resulting estimates of  $\bar{c}$  were .00068 for S and .00109 for EC. For  $(1 - h^2) \sigma^2 = .178$ , the resulting estimates of  $\bar{c}(1 - h^2) \sigma^2$  were .00012 for S and .00019 for EC. Assumptions implicit in these approximations are discussed by Kennedy (1990).

Resulting means and SE including drift for EBV of ewes mated in 1993 were  $.070 \pm .032$  for S and  $.033 \pm .023$  for EC. Selection response in S thus approached significance ( $P = .08$ ). Hill (1972) indicated that the regression of cumulative response on cumulative selection differential was a more sensitive estimator of realized heritability than the ratio of total response to total selection differential when heritability is low. Thus, conclusions regarding significance of genetic trends based only on ewes bred in 1993 may be conservative.

Trends in permanent environmental effects on fertility were positive for S and EC (Table 2), but they were small. Service sire trends (Table 2) were

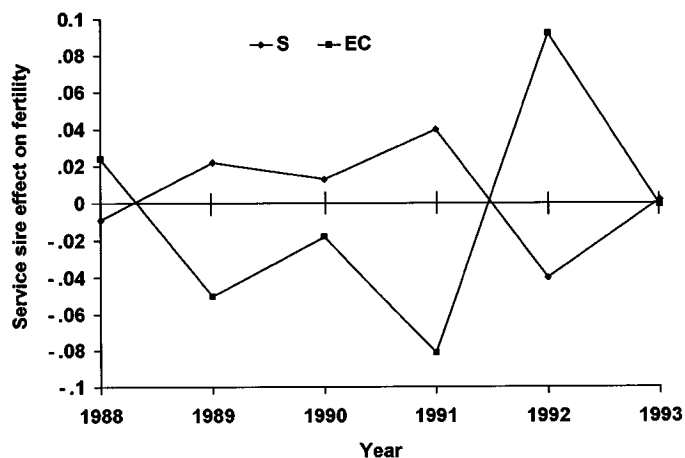


Figure 3. Mean service sire effects on fertility for S and EC in each year.

negative for S and positive for EC. Large variation in service sire effects across years (Figure 3) points out the risk inherent in single-sire matings during suboptimal breeding seasons. The poor performance of S rams in 1992 reflects the only year in which the 7- to 8-mo-old ram lambs differed in fertility from older rams.

These results suggest a modest positive genetic response to selection for fertility of approximately .014/yr coupled with a small response in mean permanent environmental effects due to continued culling of ewes. Documentation of selection response for lowly heritable traits in species with long generation interval and overlapping generations is challenging in experiments of reasonable duration. Based on previous literature (Hanrahan and Quirke, 1986; Fahmy, 1990), we had anticipated that heritability of fertility would be higher in fall lambing than in spring lambing. However, that was not the case. The heritability estimate of .07 used in this study (Al-Shorepy and Notter, 1996) was similar to the average value of .06 reported for fertility by Fogarty (1995). However, phenotypic variance in fertility of .190 was much larger than that expected in fall matings, allowing for substantial additive genetic variance within the flock. Still, when accounting for genetic drift, this 6-yr, 1.45-generation experiment was at best minimally sufficient to document selection response in the S flock.

**Time Trends in Correlated Traits.** Genetic trends in litter size (Figure 4) were positive in S and EC but larger in S. The small positive trend in EC may reflect sampling and/or natural selection because essentially all ewe lambs born in GC were used as replacements. Genetic trends in fall litter size in S suggest a positive association with fertility, in agreement with the estimate of the additive genetic correlation between spring fertility and fall litter size of .56 reported by Al-Shorepy and Notter (1996) for

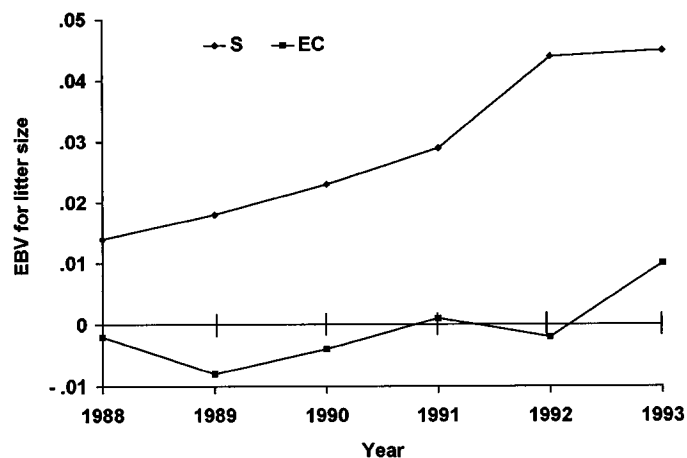


Figure 4. Genetic trends in litter size EBV for ewes mated in S and EC in each year.

this population. No trends in permanent environment for litter size were observed in either flock.

Genetic trends in litter size in this study were larger than the value of .0028 lambs/yr reported by Bhuiyan and Curran (1993) for Romney Marsh sheep selected for prolificacy and litter size using mixed-model techniques. Bradford (1985) reported that theoretical and realized maximum rates of response to direct selection for litter size were approximately .02 lambs/yr. Correlated responses in litter size in S in the current study would be approximately 40% of that value.

Nonsignificant genetic trends in birth weight were observed in S or EC. However, positive genetic trends in maternal weaning weight and 90-d weight were observed in S and EC (Table 2). Positive genetic trends in weaning weight were also observed in EC but not in S, whereas positive genetic trends in 90-d SC were observed in S but not EC. These trends likely primarily reflect responses to selection for body size and SC in ram lambs chosen for breeding. Al-Shorepy and Notter (1996) reported a genetic correlation of  $-.31$  between fertility and 90-d weight in this population, but this negative association was apparently overcome by modest selection of ram lambs on body size. However, the larger genetic trends in weaning weight in EC relative to S may represent an earlier manifestation of this negative relationship. The larger genetic trend in 90-d SC in S is consistent with the greater emphasis placed on SC in the breeding soundness examination for 7-mo-old ram lambs in S compared to 14-mo-old ram lambs in EC and with the genetic correlation of .29 between fertility and 90-d SC reported by Al-Shorepy and Notter (1996).

Correlated responses in fall litter size suggest that this trait may provide useful information to supplement direct selection for fertility. Two possible explanations for this response can be put forward. The first

is a general explanation: animals in this population with higher fecundity may in general also be more fertile in spring. However, ovulation rate and litter size per ewe lambing are known to also show seasonal variation and to be reduced in fall lambing (Hulet et al., 1974; Notter and Copenhaver, 1980; Lewis et al., 1996). Thus an alternative, and perhaps more likely, explanation for the observed correlated response is that ewes that are less seasonal also experience smaller seasonal depressions in ovulation rate and litter size.

*Realization of Selection Differentials for Fertility.* Estimates of genetic trend based on mean EBV from BLUP analyses with nonzero heritability measure a combination of selection differentials applied and realized selection response. In order to focus more directly on selection response, two EBV were calculated for each of the 330 S and EC ewe lambs entering the study: a pedigree EBV available before first breeding and a realized EBV calculated using only data that accrued after calculation of the pedigree EBV. Initially, all relationships present in the data were used to derive the pedigree and realized EBV. The resulting regression of realized EBV on pedigree EBV was  $.20 \pm .08$  ( $P = .01$ ). If pedigree and realized EBV reflect the same trait, the expected value of this regression coefficient is approximately equal to the squared accuracy of the realized EBV (Notter and Diaz, 1993), where accuracy is defined as the theoretical correlation between true breeding value and the realized EBV given the analytical model. The mean accuracy of the realized EBV for these ewe lambs ranged from .50 for ewes born in 1988 to .33 for ewes born in 1992 and averaged .43. Squared accuracies on the order of .25 to .10 thus correspond well to the observed regression coefficient of .20. These results indicate that pedigree EBV adequately predicted subsequent performance.

The significant regression coefficient observed between pedigree and realized EBV provides strong, but not necessarily unequivocal, evidence of a genetic basis for spring fertility. When all relationships in the data are used to calculate pedigree and realized EBV, data from dams contribute to both EBV. Even though different data are used, if repeatability of spring fertility is greater than zero but heritability is not (i.e., if only permanent environmental variance is greater than zero), then repeatable future performance of dams of ewe lambs used in the regression analysis could lead to correlation between pedigree and realized EBV. To circumvent this potential problem, realized EBV were recalculated ignoring maternal relationships present before birth of the lambs. The resulting regression coefficient was reduced to  $.13 \pm .07$  in accord with the reduced accuracy of the realized EBV and, under these more stringent analytical conditions, now only approached significance ( $P = .09$ ). Results of these supplemental

analyses were thus consistent with the more comprehensive estimates of genetic trends from Table 2.

Finally, in each year, EBV were calculated at the start of the breeding season and compared within year, breeding pasture, and ewe age class for ewes that subsequently did or did not lamb. Overall effects of EBV as a predictor of future fertility were positive. The EBV for ewes that lambed averaged  $.019 \pm .004$  higher than EBV of open ewes ( $P < .01$ ). The small absolute value of this difference must be interpreted in the light of the limited range in EBV. The EBV are regressed values and averaged .038 with a SD of only .049. Thus, the observed difference of .019 corresponds to .39 standard deviations in EBV. Some breeding rams had low fertility, so data were also reanalyzed after removing data on eight rams with fertility of less than .20 and then data on an additional nine rams with fertility of less than .30. However, the results did not change. The predictive ability of EBV tended to differ for ewes of different ages ( $P = .09$ ). The difference in EBV between pregnant and nonpregnant ewes was largest (.028) for adult ewes (third and greater exposures). Differences were smallest in 7-mo-old ewe lambs (.006) and in ewes at their second exposure (.009) and were intermediate in 14-mo-old EC ewe lambs (.014).

## Implications

Selection for fertility in an annual fall lambing system resulted in increases in estimated breeding value (EBV) for fertility and in correlated increases in fall litter size. Pedigree estimates of EBV for fertility were positively associated with future performance, and fertility EBV were significantly associated with future fertility. These results suggest that performance in fall lambing can be improved by selection.

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