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Genetic variation in uterine efficiency and differential responses to increased ovulation rate in sheep

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ABSTRACT

Genetic variation in ovulation rate, both within and between breeds, is recognised as a major source of variation in litter size, while breed differences in embryonic survival are generally assumed to be unimportant. Results reported here for several trials, years and locations and involving large numbers of naturally multiple ovulating ewes show significant and consistent genetic differences in the proportion of ewes producing 2 lambs following conception to twin ovulations (uterine efficiency).

Compared to contemporary Romneys (uterine efficiency = 0.59), 4 to 34% more ewes of 5 other genotypes produced twin lambs following conception to twin ovulations. At the extreme, Border Leicester × Romneys ranged from 24 to 52% superior in 3 comparisons. At ovulation rates higher than 2, inter-ovarian ovulation pattern was also found to influence litter size. Increasing disproportionality of ovulation rate between ovaries resulted in lower litter size. This may be due to uneven distribution of implantation sites and increased losses due to crowding.

Keywords Uterine efficiency; ovulation rate; embryo survival; litter size; sheep reproduction; ovulation pattern

INTRODUCTION

Variation in litter size of sheep has been shown to result primarily from variation in ovulation rate. Accordingly management regimes to increase ewe mating weights or to 'flush' ewes immediately prior to mating are aimed at increasing flock mean ovulation rates, with little evidence of differential embryonic survival over treatments.

Genetic differences in litter size among breeds are likewise associated with differential ovulation rates (Larson and McDonald, 1971; Meyer, 1979) and successful selection for increased litter size has given marked correlated responses in ovulation rate (Trounson and Moore, 1972; Meyer and Clarke, 1982).

Estimates of breed differences in uterine efficiency have been severely limited by the small numbers of ewes lambing to multiple ovulations. Large ewe numbers are even more critical in efforts to examine the marginal effects on litter size of increasing ovulation rates to multiples beyond twin ovulations and in assessing the effect of inter-ovarian ovulation pattern on litter size.

EXPERIMENTAL DESIGN

Ovulation rate data were collected from several ewe genotypes at 3 research stations. Ewes were examined via laparoscopy 3 to 7 days post mating and the number of corpora lutea on each ovary was recorded. Ewes were re-examined at any subsequent returns to service during the 6-week mating period so that lambing results could be related back to ovulation rate at the specific oestrus of conception. The locations and genotypes examined are given in Table 1 and described in further detail as follows:

Crater (1978)

Nine genotypes of F_1 ewes sired by local and exotic ram breeds and all out of Romney dams were examined. All ewes (about 1300) were slaughtered in late pregnancy at the termination of the exotic sheep evaluation trials and the number of foetuses determined (Meyer, 1979). Results are given here for 4 of the genotypes which have been examined at other locations subsequently. The Romney, Border Leicester (BL) and Cheviot-sired genotypes were represented by two-, four- and six-tooth ewes while only two-tooth Booroola × Romney (B × R) ewes were present.

Tokanui (1981 and 1982)

Romney, interbred BL × Romney and BL ewes of 4 age groups (two-tooth to 5-year-old) were randomly sampled from their respective selection flocks in each of 2 successive years. Background of the lines was described by Meyer and Clarke (1982). Since the ewes of 3 of the birth years could contribute data in both trial years, only the first lambing record of such ewes was included in analyses. Hence, the 2 years' data could be regarded as independent.

Rotomahana (1981 and 1982)

Straightbred and Booroola-sired F_1 ewes from Romney and Perendale dams were examined as two-tooths in each year and as four-tooths in 1982. Only the first record of ewes conceiving to twin ovulations in both years was used. The 3 resulting year-age data sets were considered independent for deriving estimates of breed difference in uterine efficiency.

Routine lambing information including dam identity, litter size, and lambing date were recorded at Rotomahana and Tokanui. Lambing dates were compared with mating dates as a check on oestrus of conception before comparing ovulation rates with litter size. Any questionable data were discarded. Likewise, any record of litter size exceeding ovulation rate was excluded from the analysis since it was generally impossible to determine the cause of discrepancy.

Since ewes must produce a minimum of 1 foetus in order to be considered in investigations of uterine efficiency, only multiple ovulating ewes can provide information on the marginal effect of additional ova on litter size. Thus, uterine efficiency of ewes conceiving to twin ovulations is defined here as the proportion of such ewes producing 2 lambs. Similarly, uterine efficiency of triple ovulating ewes is the increased litter size over twin ovulators, i.e., the marginal response to the third egg, and similarly for quadruple ovulators.

Breeds were compared on the basis of ewes conceiving to twin ovulations. Uterine efficiency was regarded as binomially distributed and analysed by a generalised linear model (GLIM; Nelder and Wedderburn, 1972) employing maximum likelihood procedures. All breeds were compared to contemporary Romneys present in appropriate years and locations.

In addition, 1982 litter size and ovulation rate data from two-tooth and four-tooth B × R and B × P ewes were used to estimate marginal response to ovulation rates of 3 or 4 ova and to examine the effect of inter-ovarian ovulation pattern on litter size. Litter size was analysed by least squares analysis of variance procedures treating year, breed and ovulation pattern as fixed effects.

RESULTS

Mean litter size is given in Table 1 for 982 ewes of various genotypes conceiving to twin ovulations. The highest 'twinning success' among Romneys was achieved at Crater, possibly assisted by the positive identification of every lamb to its dam. Tokanui success has been lowest with less than half of those Romney ewes conceiving to twin ovulations producing 2 lambs.

The same results are given in Table 2 based on the proportion of twin-ovulating ewes producing 2 lambs (uterine efficiency) relative to contemporary Romneys at each location. Relative to Romneys, uterine efficiency was higher for BL × Romneys ($P < 0.01$), Booroola × Perendales ($P < 0.05$), BL ($P < 0.10$) and Cheviot × Romneys ($P < 0.10$). B × R ewes were only slightly above Romneys.

Mean litter sizes in 1982 for B × R and Booroola × Perendale (B × P) ewes are given in Table 3 for over 300 ewes lambing to multiple ovulation rates of 2 to 4.

TABLE 1 Mean litter size (and number) of ewes conceiving to twin ovulations.

	Crater	Tokanui		Rotomahana			
	1978	1981	1982	1981	1982 (two-tooth)	1982 (four-tooth)	Mean
Romney	1.71 (31)	1.51 (41)	1.46 (35)	1.63 (43)	1.54 (52)	1.67 (64)	1.59
Cheviot × Romney	1.74 (54)	—	—	1.66 (29)	1.71 (83)	1.74 (68)	1.67
BL × Romney	1.88 (69)	1.69 (51)	1.70 (46)	—	—	—	1.79
BL	—	1.57 (42)	1.66 (36)	—	—	—	1.72
Booroola × Romney	1.75 (28)	—	—	1.62 (39)	1.56 (36)	1.71 (24)	1.61
Booroola × Perendale	—	—	—	1.74 (42)	1.76 (41)	1.88 (24)	1.77

TABLE 2 Uterine efficiency of twin-ovulating ewes of various genotypes relative to the Romney.

	Crater	Tokanui		Rotomahana				
	1978	1981	1982	1981	1982 (two-tooth)	1982 (four-tooth)	Mean	
Romney	100	100	100	100	100	100	100	
Cheviot × Romney	104	—	—	105	131	110	114	†
BL × Romney	124	135	152	—	—	—	134	**
BL	—	112	143	—	—	—	122	†
Booroola × Romney	106	—	—	98	104	106	104	ns
Booroola × Perendale	—	—	—	117	141	131	131	*

Comparisons to Romney (mean uterine efficiency = 0.59).
† ($P < 0.10$).

Results are further sub-divided to examine any litter size effect due to inter-ovarian distribution of ova within each ovulation rate class. Mean litter size adjusted for multiple ovulation rate was higher for B × P than B × R ewes ($P < 0.05$). There was no age of ewe effect. Mean litter size was higher for B × P ewes for both twin and triple ovulations, over both age groups and both ovulation patterns within each ovulation rate category. The same breed ranking also applied for the largest group of quadruple ovulators (born 1979 ewes with 3-1 ovulation patterns) and for quadruple ovulators pooled across ages and ovulation patterns.

The ratio of ovulation patterns within each ovulation rate was consistent with independent occurrence of ovulation between ovaries, i.e., the proportion of 1-1 to 2-0 ovulations among twin ovulators was similar.

There was no evidence of differential reproductive success between the 2 ovulation patterns for twin ovulators. At higher ovulation rates, however, ovulation patterns giving more equal distribution of ovulations over both ovaries resulted in higher litter size than disproportionate patterns. Thus, the marginal response of litter size to ovulation rate depended not only on the initial ovulation rate and ovulation pattern but also the resulting ovulation pattern. For twin and triple ovulating ewes, adding 1 ovum to the ovary with fewer ova gave a greater marginal response than adding the ovum to the ovary already more productive. The least squares marginal responses to additional ova are shown in Fig. 1.

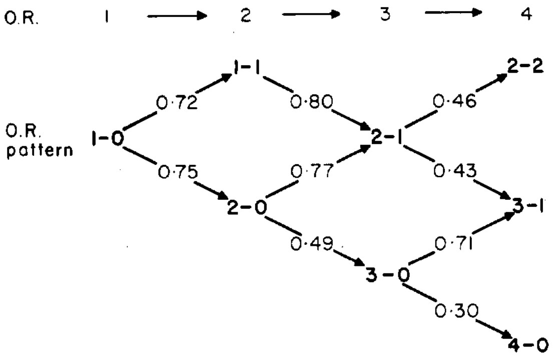

FIG. 1 Ovulation pattern effects on marginal litter size response to increased ovulation.

DISCUSSION

Numerous embryo transfer experiments (e.g., Larson and McDonald, 1971; Bradford *et al.*, 1974) have failed to find significant breed differences in litter size when the same number of eggs (varying from 2 to 6 between trials) have been transferred to different recipient breeds. Generally, the number of recipient ewes involved in individual embryo transfer studies reported has been modest and the power of statistical tests so low that only large differences would have been detected. One might also question whether embryo transfer techniques might not in themselves reduce any between-breed differences.

Results from this trial with large numbers of naturally ovulating, non-synchronised ewes clearly indicate that genetic differences in uterine efficiency do exist between breeds for twin ovulating ewes. Romneys consistently produced fewer lambs following conception to twin ovulations, the 5 other genotypes averaging from 4 to 34 more lambs per 100 ewes lambing. Additional supporting data from Crater found uterine efficiency of the Romney lowest of all 9 ewe genotypes examined with Finn × Romney ewes highest (Meyer, 1979). Larson and McDonald (1971) likewise found lower litter size for Romney ewes when they were compared to BL × Romney crosses after each had received 3 embryos (R = 1.86 *v* BL × R = 2.12). Effects of ewe age on uterine efficiency were inconsistent over years and locations. It would appear that season and age effects on uterine efficiency are small relative to their typical effects on ovulation rate.

The variation in uterine efficiency of Romneys across locations is unexplained. At all locations

TABLE 3 Mean litter size (and number) of Booroola-cross ewes conceiving in 1982 to multiple ovulations of differing inter-ovarian ovulation patterns.

Ovulation rate	Ovulation pattern*	Four-tooth B × R	Four-tooth B × P	Two-tooth B × R	Two-tooth B × P	Mean
Twin	1-1	1.76 (17)	1.87 (23)	1.44 (18)	1.79 (23)	1.72
	2-0	1.67 (21)	1.94 (18)	1.67 (18)	1.71 (17)	1.75
Triple	2-1	2.38 (16)	2.64 (22)	2.45 (11)	2.54 (13)	2.52
	3-0	2.00 (3)	2.50 (4)	2.00 (4)	2.45 (11)	2.24
Quadruple	2-2	3.25 (4)	3.17 (6)	2.00 (4)	3.67 (3)	2.98
	3-1	2.83 (18)	2.92 (12)	2.67 (6)	3.33 (3)	2.95
	4-0	2.67 (3)	1.67 (3)	3.00 (2)	2.50 (2)	2.54

* 3-1 indicates 3 corpora lutea on 1 ovary, 1 on the other.

Romney ewes were the progeny of rams and ewes sampled widely across the industry, so differences are unlikely to be genetic.

The more detailed examination of Rotomahana data for the Booroola crosses in 1982 (Table 3) not only shows a consistent genetic effect across both ovulation rates and ovulation patterns within ovulation rates, but also indicates an effect of ovulation pattern on litter size. The results clearly suggest that uterine efficiency declines as the imbalance of ovulations between ovaries increases. Results from smaller numbers of triple ovulating ewes pooled across breeds at Crater (68 ewes), Tokanui in 1981 (21 ewes), Tokanui in 1982 (46 ewes), Rotomahana in 1981 (65 ewes) and Rotomahana Romneys and Perendales (38 ewes) in 1982, found bilateral (i.e., 2-1) ovulations produced more lambs than unilateral ovulations in 4 of the 5 trials. Across the 5 trials the average advantage to bilateral ovulators was 0.41 lambs compared to 0.28 lambs for Rotomahana Booroola crosses in 1982 (Table 3). Hence the effect is not merely a manifestation of Booroola breeding.

The effect of ovulation pattern on litter size may be associated with post implantation distribution of embryos between the 2 uterine horns, with disproportionate ovulation patterns leading to increased embryonic crowding and possibly lower resulting litter size at lambing.

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