OVULATION RATE AS THE SELECTION CRITERION FOR LITTER SIZE IN SHEEP

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SUMMARY

Egg transfer experiments have consistently failed to find differences among sheep breeds in their ability to support a given number of fertilised eggs. The literature on egg survival rate in pregnant, multiple ovulating ewes is also remarkably consistent across a wide range of breeds and environments in terms of the ratio of foetuses (or lambs) to corpora lutea. Two reports on egg survival in ewes of the same breed but genetically different ovulation rates have also failed to demonstrate differences in egg survival. It is concluded that there is no gentic variation among ewes in their ability to support a given number of fertilised eggs (within the range l-6). It follows, therefore, that the genetic correlation between litter size and ovulation rate is unity. Consequently, selection for increased litter size is really using litter size as an index of ovulation rate. It is shown that the efficiency of this index is a function of average ovulation rate and declines as ovulation rate increases.

INTRODUCTION

The heritability of litter size in sheep has generally been found to be less than 0.1 and consequently the rate of change from selection will be slow. An additional limitation in selecting for increased litter size is the discrete nature of the trait which can mean that actual selection pressure is less than would be possible with a continuous variable (Hanrahan 1974). Use of repeated records will increase heritability and give more opportunity to optimise the selection differential. However, the generation interval will be increased. Ovulation rate can be measured (by laparoscopy) at successive cycles within the same breeding season and hence the benefits of repeated records can be obtained without any increase in the generation interval. For these reasons and the expectation that the heritability of ovulation rate would exceed that for litter size Hanrahan (1974) proposed that selection for increased litter size should be based on ovulation rate. There was very little information available at that time on the repeatability of ovulation rate and none on heritability. The situation has changed in the interim.

Table 1 contains a summary of repeatability and heritability estimates for ovulation rate and litter size in Galway and Finnish Landrace (Finn) ewes (Hanrahan 1974, 1979). The low repeatability of litter size in the Finn stands in stark contrast with the very high repeatability of ovulation rate in this breed.

TABLE 1 Parameters of litter size and ovulation rate in two sheep breeds

Parameter	Breed	
	Finn	Galway
Mean-Ovulation rate	3.8	1.7
-Litter size	2.6	1.5
Repeatability-Ovulation rate	0.67	0.30
-Litter size	0.10	0.20
Heritability -Ovulation rate	0.45±0.07	0.57±0.28
-Litter size	0.10±0.04	0.06±0.03

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This finding prompted an examination of the relationship between ovulation rate and litter size, within populations which vary in mean ovulation rate, and the problem of predicting the response in litter size when selection is for increased ovulation rate.

MATERIALS AND METHODS

Ovulation rate data have been collected on Finn and Galway ewes, and crosses and backcrosses involving these two breeds. Generally ovulation was at a controlled oestrus following treatment with an intravaginal pessary impregnated with progestagen. Corpora lutea were counted either at laparotomy or by laparoscopy. Any ewe which failed to ovulate was excluded from the data prior to analysis.

Uterine capacity

The problem of predicting the correlated response in litter size from selecting on ovulation rate raises the question of genetic variation in uterine capacity which is defined as the probability of egg survival given the number of fertilised eggs entering the uterus. Egg transfer experiments in our laboratory (with up to six eggs per recipient) have failed to find breed differences in uterine capacity (Hanrahan & Quirke 1976, 1977) and this result is consistent with other egg transfer studies involving different breeds (Larsen & McDonald 1971; Lawson & Rowson 1972; Bradford et al. 1974). Divergent selection for litter size in the Merino breed was successful but did not change uterine capacity (Trounson and Moore 1972) and the divergence in ovulation rate exceeded that observed for litter size. Bindon et al. (1978) found no difference in uterine capacity following the transfer of three eggs to Merino and Booroola Merino recipients which had ovulation rates of 1.5 and 4.0 respectively. In a selection experiment for increased litter size in Galway sheep (Hanrahan and Timon 1978) the response in ovulation rate exceeded the response in litter size (Hanrahan 1979).

The literature reviewed here clearly indicates that genetic variation in uterine capacity can only play a very minor role in variation in litter size. In our egg-transfer work the genotype of the egg has consistently failed to influence its survival in utero (Hanrahan and Quirke 1980). Consequently the genetic correlation between ovulation rate and litter size is taken as being unity.

Predictins litter size

Accurate prediction of litter size from ovulation rate depends on knowing the distribution of ovulation rate and the probability of egg survival as a function of the number of eggs shed and must take into account fertilisation failure and returns to service due to early embryonic death. Fertilisation may be considered an all-or-none phenomenon (Restall et al. 1976) and it is assumed that fertilisation failure is independent of the number of ova shed. Under these conditions ewes which return to service due to fertilisation failure are a random sample of all ewes and consequently will have the same average ovulation rate at the next oestrus. Ewes with two or three fertilised ova are less likely to lose all embryos than ewes with a single fertilised ovum and, consequently, ewes returning to service due to early embryo mortality will have an average ovulation rate which is expected to be less than the population mean. As a consequence of the phenomenon of regression towards the mean the average ovulation rate of this group is expected to increase at the next cycle. If we assume that average ovulation rate does not change between adjacent cycles then little error is introduced by ignoring the non-random composition of the group of ewes which return to service. Estimates of embryo survival in pregnant ewes (from Hanrahan 1979) as a function of ovulation rate (Table 2) were combined with data on the distribution of ovulation rate observed in different groups of sheep to construct a curve relating average ovulation rate and average litter size (Fig. 1).

TABLE 2 Summary of literature on egg survival in pregnant ewes

No. corpora lutea (n)	No. ewes (N)	Survival rate[a] (k)	Embryo loss rate[b] (q)
2	2642	0.84	0.18
3	345	0.75	0.27
4	75	0.66	0.35
5	19	0.65	0.35
6	10	0.47	0.54
7	14	0.34	0.69

[a] Calculated as total embryos ÷ (n x N)

[b] Obtained by solving the equation $1 - q = k\ (1-q^n)$

The correlation between litter size and ovulation rate

With an additional assumption that the distribution of viable embryos, given ovulation rate and embryo survival rate, is binominal a joint frequency distribution may be constructed for ovulation rate and litter size. This was done for a range of population mean ovulation rates and the resulting relative frequencies were scaled to eliminate the zero litter size class. These joint frequency distributions were used to calculate the correlation between litter size and ovulation rate.

RESULTS AND DISCUSSION

It is clear from Fig. 1 that the relationship between variables is curvilinear although not markedly so as average ovulation rate changes from 1.5 to 2.5. Over this range a unit change in ovulation rate will result in an increase of approximately 0.6 in average litter size. The curve tends towards a

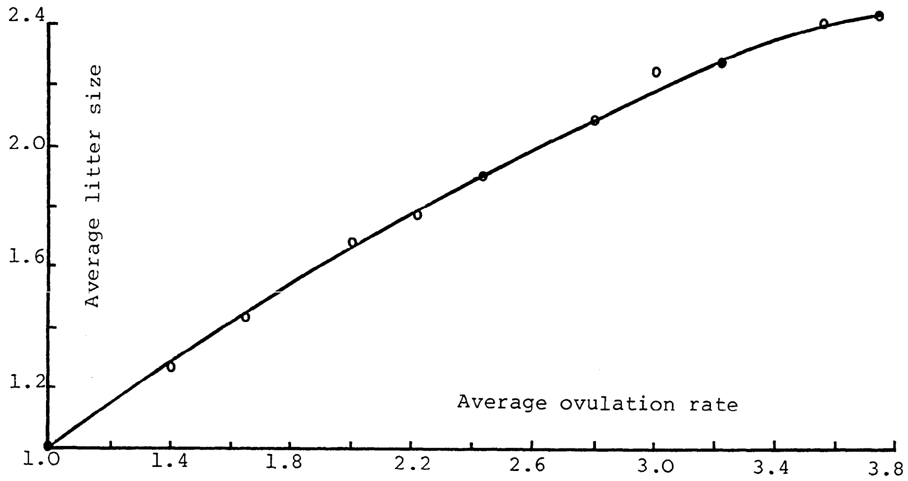

Fig. 1. Predicted relationship between average ovulation rate and average litter size.

plateau which would represent maximum uterine capacity. The exact form of the curve is a function of the set of egg survival probabilities used as well as the distribution of ovulation rate. The curve may be used to transform predicted response to selection for ovulation rate into the correlated changes to be expected in litter size.

The correlation between the number of eggs shed and litter size is shown in Table 3 as a function of average ovulation rate and the table also shows the corresponding average litter size. The correlation declines as average ovulation rate increases. The notable feature of the results is that even in populations with low average ovulation rate litter size is only capable of "explaining" about 50 percent of the variation in ovulation rate. This means that ovulation rate should be used as the selection criterion when genetic selection is to be used to change litter size. The efficiency of litter size as a selection criterion relative to ovulation rate is given by the correlation coefficients in Table 3.

TABLE 3 Correlation between number of eggs shed and litter size

Population mean		
Ovulation rate	Litter size	Correlation coefficient
1.40	1.28	0.76
1.64	1.43	0.72
2.21	1.78	0.61
2.43	1.91	0.58
2.80	2.10	0.55
3.56	2.41	0.41

The genetic gain per unit time is a function of accuracy and generation interval. Hanrahan (1974) concluded that, since all the information required for selection on ovulation rate could be obtained in one breeding season,annual genetic gain would be twicethat possible with a comparable amount of information on litter size. This conclusion was based on the assumption of equal accuracy. It is now clear that annual genetic gain could be three times greater with selection on ovulation rate.

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