SELECTION FOR PROLIFICACY IN ROMNEY SHEEP
Ⅱ. CORRELATED RESPONSES

A. K. F. H. Bhuiyan[1] and M. K. Curran

Wye College, University of London, Wye, Ashford, Kent TN25 5AH, England

Summary

A selection experiment with Romney Marsh sheep was used to evaluate correlated responses to selection. The selected flock was formed in 1979 by the Romney Group Breeders where selection was for prolificacy, defined as the number of live lambs born per ewe joined per year and a randomly selected control flock was established in 1982. Selection for prolificacy resulted in (i) increased ewe fertility, (ii) increased ewe ovulation rate, (iii) increased ewe litter size, (iv) decreased ewe body weight, (v) decreased lamb birth weight and (vi) decreased lamb 8-week weight. The rates of correlated responses per year respectively for ewe fertility, ewe ovulation rate, ewe litter size, ewe body weight, lamb birth weight and lamb 8-week weight were 0.033 (0.002), 0.043 (0.016), 0.019 (0.005), −0.017 (0.006), −0.055 (0.025) and −0.150 (0.057).

(**Key Words** : Sheep, Selection, Prolificacy, Correlated Response)

Introduction

Prolificacy is an economic trait which determines the efficiency of meat production in sheep. Direct selection for litter size in sheep has proved to be effective (Bradford, 1985). Information on the genetic correlation between reproduction rate and some production characters is variable in sheep (Land et al, 1983; Atkins, 1986; Davis and Kinghorn, 1986; Owen et al, 1986). Realized correlated responses are of interest in sheep selection studies for checking correlations between pairs of important production characters (McGuirk et al., 1986). Absolute responses are difficult to judge, because they are influenced by both the genetic correlation and heritability of the correlated trait, and an estimate for realized genetic correlation can therefore only be obtained when realized heritability for the correlated trait would also be available (Falconer, 1989).

The realized responses to direct selection for prolificacy, defined as the number of live lambs born per ewe joined per year (LLB/EJ)in the Romney sheep have been described by Bhuiyan and Curran (1995). In this paper the realized correlated responses in some production characteristics are examined. The examined traits were ewe fertility, ovulation rate, litter size and body weight; and lamb birth and 8-week weight. Due to the lack of estimates of genetic and phenotypic parameters in the population under study, a prediction of expected correlated response was not possible.

Materials and Methods

The data used in this study were obtained over a period of 10 years (1980 to 1989 inclusive) from a selection flock of Romney sheep maintained at Wye College, Kent, England. In the 1979, the flock was established by the Romney Group Breeders (RGB), a farmer cooperative formed by 12 members of the Romney Sheep Breeders Society. The objective of the RGB was to develop a line of prolific Romney sheep to use as a source of high merit breeding stock for their own flocks-particularly males. As a result, prolificacy, defined as the number of live lambs born per ewe joined per year (LLB/EJ) was chosen as the selection criterion.

A contemporary control flock was established in 1982 and maintained in the same environment with the target of monitoring genetic progress achieved in the RGB selected flock. Details of the formation of the selected and control flock were described by Anderson and Curran (1990). The animal management procedure and the selection procedure applied in both the flocks have already been described (Bhuiyan and Curran, 1995).

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[1] Address reprint requests to Dr. A. K. F. H. Bhuiyan, Department of Animal Breeding and Genetics, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh.

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Traits measured

Ewe's fertility, ovulation rate, litter size and body weight and lamb's birth and 8-week weight were the six traits included in the analysis of correlated response to prolificacy selection. Ewe fertility was defined as whether a ewe lambed or not at a particular age or year when put to the ram (F). Thus a fertile ewe was assigned a score 1 and an infertile ewe, 0. Ovulation rate or the number of corpora lutea released by the ovaries (right and left) per oestrus cycle (O) was observed by laparoscopic operation, performed within 3-7 days of behavioural observation of oestrus. Ovulation rate was assessed primarily on ewes aging 3 years. The litter size (LS), defined as the number of lambs born per ewe lambing per year of individual ewes were recorded immediately after lambing. The body weight of ewes (M) of all ages before mating were recorded on a single day in each year.

Birth weights (B) of individual lambs were recorded immediately after lambing. There were very few (3 nos.) quadruplet lamb sets in the whole data set and these were merged into the triplet category. The 8-week weight (W8) of lambs was measured on a single day in each year. Individual raw data were first adjusted to correct for ages in days of the lambs by linear interpolation between birth and observed approximate 8-week weight (Lasslo et al, 1985) using the following formula:

Age adjusted W8 =

$$\frac{\text{Raw W8 (kg)} - \text{B (kg)}}{\text{Age at recording (in days)}} \times 56 + \text{B (kg)}$$

Statistical analysis

The data were analysed by the method of least-squares (Harvey, 1986) for investigating correlated responses with time of selection. Least-squares models were fitted to the data with all available independent variables. The usual step-down procedure was followed deleting the least-significant independent variable from the model at each run. Then the data were corrected for all the significant non-genetic fixed effects using least-squares constant estimates from the best fitting model leaving the line effect, the only genetic component in the model. Response was detected by subtracting the control line corrected mean performance from the corresponding selected line corrected mean.

The best fitting models for the traits studied were :

i) $F_{ijk} = \mu + L_i + A_j + Y_k + e_{ijk}$
ii) $O_{ijk} = \mu + L_i + Y_j + A_k + e_{ijk}$
iii) $LS_{ijk} = \mu + L_i + A_j + Y_k + e_{ijk}$
iv) $M_{ijklm} = \mu + L_i + Y_j + A_k + D_l + B_m + e_{ijklm}$
v) $B_{ijkl} = \mu + L_i + S_j + T_k + D_l + e_{ijkl}$
vi) $W8_{ijklmno} = \mu + L_i + S_j + Y_k + T_l + R_m + D_n + B_o + e_{ijklmno}$

where, μ is the overall mean, L denote line, A denote age of ewe, Y denote year of performance, S denote sex of lamb, T denote type of birth, R denote rearing type, D denote age of dam, B denote birth weight (covariate), e denote random error term.

Results

Least-squares means (standard errors) for the ewe traits are presented in table 1 and responses in ewe traits are given in table 3.

Ewe fertility

None of the independent variables had significant effect on ewe fertility (table 1). The estimate of correlated response in ewe fertility was 0.03 (s.e. 0.02) which was not significant (table 3). Such a correlated positive change in ewe fertility would lead to a genetic change of 0.003 (s.e. 0.002) and 0.004 (s.e. 0.003) per year and year of birth respectively.

Ewe ovulation rate

The ovulation rate of the selected line ewes was significantly ($p < 0.01$) higher than the contemporary control ewes (table 1). But ovulation rate did not differ significantly between age of the ewe sub-classes. Selection for prolificacy has resulted in positive genetic changes in ovulation rate (table 3). The overall response of 0.39 (s.e. 0.14) corpora lutea per oestrus cycle between the selected and control ewes was statistically significant ($p < 0.01$). This difference was obtained by analysing one record per ewe and was attained by selection in the year of births from 1980 through to 1986 and year 1979 to 1988 which represent some 9 years of selection. Such a divergence averages an improvement on the scale of 0.055 (s.e. 0.020) and 0.043 (s.e. 0.016) corpora lutea per ewe per year of birth and year respectively.

Ewe litter size

Litter size was significantly effected by line, age of ewe and year of performance (table 1). A difference of 0.17 (s.e. 0.04) lamb between selected and control ewes (table 3) was observed which was statistically highly significant ($p < 0.001$). This correlated response in litter size when expressed per annum and per year of birth represents respectively 0.017 (s.e. 0.004) and 0.021 (s.e. 0.005) lambs.

TABLE 1. LEAST-SQUARES MEANS (S.E.) FOR EWE TRAITS

	Fertility ($R^2 = 0.11$)	Ovulation rate ($R^2 = 0.14$)	Litter size ($R^2 = 0.09$)	Body weight ($R^2 = 0.76$)
Overall	0.93 (0.01)	1.99 (0.15)	1.72 (0.04)	74.64 (0.63)
Line		**	***	*
Selected	0.95 (0.01)	2.18 (0.16)	1.86 (0.04)	73.89 (0.62)
Control	0.92 (0.02)	1.79 (0.17)	1.63 (0.05)	75.39 (0.78)
Age of ewe (yrs)			***	***
2	0.95 (0.01)		1.52 (0.03)	59.51 (0.47)
3	0.93 (0.02)	2.22 (0.13)	1.67 (0.04)	70.42 (0.50)
4	0.91	1.75 (0.38)	1.79 (0.05)	77.75 (0.63)
5			1.83 (0.06)	80.27 (0.76)
6			1.73 (0.09)	79.59 (1.23)
6+			1.76 (0.17)	80.32 (2.92)
Year of performance			*	***
1983	0.91 (0.03)		1.78 (0.08)	67.58 (1.21)
1984	0.94 (0.02)	2.82 (0.32)	1.74 (0.07)	72.79 (1.03)
1985	0.96 (0.02)	1.80 (0.26)	1.63 (0.06)	78.00 (0.92)
1986	0.93 (0.02)	1.82 (0.27)	1.75 (0.06)	74.91 (0.83)
1987	0.93 (0.02)	1.74 (0.25)	1.67 (0.05)	79.43 (0.72)
1988	0.92 (0.02)	1.75 (0.26)	1.78 (0.05)	75.52 (0.80)
1989			1.65 (0.06)	74.27 (0.78)
Age of dam (yrs)				***
2				76.08 (0.92)
3				73.90 (0.76)
4				75.38 (0.74)
5				75.65 (0.81)
6				73.19 (0.86)
7				73.84 (1.16)
Birth weight (kg)				***
		Regression	linear	b = 2.96 (0.31)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Ewe body weight

Analysis of ewe body weight indicated that the control ewes were significantly ($p < 0.05$) heavier than selected ones (table 1). When corrected for environmental effects the estimates of realized response was -1.50 kg (s. e. 0.57) per ewe (table 3) which was highly significant ($p < 0.01$). The data for ewe body weight represented 8 year of births (1980-1987) spanning a total of 10 years of selection. Therefore, these estimates lead to decrease of 0.150 (s. e. 0.057) and 0.188 (s. e. 0.072) kg in ewe body weight per ewe per year and year of births of selection respectively.

Least-squares means (standard error) and responses in lamb traits are respectively given in table 2 and table 3.

Lamb birth weight

Lambs born in the control line were significantly ($p < 0.01$) heavier than those in the selected line. Age of dam had a highly significant ($p < 0.001$) effect on lamb birth weight. Males were significantly ($p < 0.001$) heavier than females and singles were significantly ($p < 0.001$) heavier than multiple births. The response was a decrease of 0.16 kg (s.e. 0.05) and this decrease was statistically significant ($p < 0.01$). Such a divergence was realized after 9 years of selection which represented seven dam year of births (1980 to 1986). Therefore, the above estimates indicate a decrease in lamb birth weight of 0.017 kg (s.e. 0.006) and 0.022 kg (s.e. 0.008) per lamb per year and dam year of birth respectively when selection was for prolificacy (LLB/EJ) in the RGB selected flock.

TABLE 2. LEAST-SQUARES MEANS (S.E.) FOR LAMB TRAITS

	Birth weight ($R^2 = 0.56$)	8-week weight ($R^2 = 0.52$)
Overall	4.98 (0.04)	21.26 (0.24)
Line	**	*
Selected	4.90 (0.04)	21.01 (0.24)
Control	5.90 (0.06)	21.51 (0.30)
Sex	***	***
Male	5.10 (0.05)	22.04 (0.27)
Female	4.86 (0.05)	20.88 (0.25)
Castrated male		20.85 (0.36)
Birth type	***	*
Single	5.99 (0.06)	22.28 (0.36)
Twin	4.95 (0.04)	20.87 (0.30)
Triplet	4.00 (0.07)	20.63 (0.47)
Rearing type		*
Single		21.76 (0.38)
Multiple		20.75 (0.27)
Age of dam (yrs)	***	***
2	4.64 (0.05)	20.64 (0.24)
3	5.01 (0.04)	21.27 (0.23)
4	5.04 (0.05)	21.69 (0.27)
5	5.09 (0.06)	21.94 (0.34)
6	5.25 (0.11)	21.63 (0.52)
7	4.85 (0.19)	20.38 (0.85)
Year of performance		***
1983		19.50 (0.50)
1984		21.29 (0.37)
1985		21.60 (0.34)
1986		23.49 (0.30)
1987		20.87 (0.27)
1988		20.80 (0.29)
Birth weight Regression linear		b = 1.26 (0.14)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Lamb 8-week weight

There were significant ($p < 0.05$) differences in lamb 8-week weights between the selected and control lines. In other words, the control line born lambs were significantly heavier than selected ones at this age. A response of -0.50 kg (s.e. 0.23) was realized which was statistically significant ($p < 0.05$). This estimate indicate an equivalent genetic change of -0.06 (s.e. 0.03) and -0.07 kg (s.e. 0.03) per lamb per year and dam year of births of selection respectively in the RGB selected flock.

Discussion

Ewe fertility

Ewe fertility is a combined trait controlled by the genotype of both the ewe and the ram. The ewes oestrous activity and the sexual drive and sperm fertility of rams also have a direct effect on its expression. A poor fit ($R^2 = 0.11$) of the least-square model to the ewe fertility data indicates that much of the variation remained unaccounted. It could be explained as a sampling effect. The results in ewe fertility lend supportive evidence to positive correlated responses by Wallace (1964) and Clarke (1972) in New Zealand Romney, Bradford et al (1981) in Targhee, Hanrahan (1984) in Galway and Atkins (1980) in Australian Merino sheep.

Ewe ovulation rate

The non-significant effect of age of ewe on ewe ovulation rate could be due to sampling effect, because the number of ewes in the 4-year subclass was comparatively much smaller or simply too few control ewes per class to achieve significance. Positive correlated changes in ovulation rate obtained in this study when selecting for prolificacy are in agreement with the results of Meyer and Clarke (1982), Hanrahan (1984) and Quirke et al (1985). The scale of change of ovulation rate obtained in this study indicates its high positive genetic correlation with prolificacy which agrees well with Hanrahan (1980). It also supports Hanrahan's (1984) contention that response will be much higher if selection is based on ovulation rate rather than prolificacy. The rates of realized response in prolificacy per year of birth female group and per year were respectively 0.026 and 0.021 lambs (Bhuiyan and Curran, 1995). Much higher rates of response (more than double) in ovulation rate than in the trait directly selected for (i. e. prolificacy) support Meyer's (1985) statement that selection for prolificacy or litter size operates primarily through changes in ovulation rate.

Ewe litter size

The selection for prolificacy resulted in significant positive gain in litter size. An annual response of 0.017 lambs per ewe lambing when selection was for prolificacy indicates a positive genetic correlation between the two traits as expected. A similar positive response of nearly the same scale in litter size was observed in the Ruakura fertility flock (Clarke, 1972) and Merino flock (Turner, 1978) where respectively New Zealand Romneys and Australian Merinos were selected for high incidence of multiple births.

TABLE 3. CORRECTED MEANS AND RESPONSE IN EWE AND LAMB TRAITS

Trait	Corrected means		Response (S.E.)	Significance of response
	Selected	Control		
Ewe Traits :				
Fertility	0.95	0.92	0.03 (0.02)	NS
Ovulation rate	2.18	1.79	0.39 (0.14)	**
Litter size	1.81	1.64	0.17 (0.04)	***
Body weight	74.67	76.17	−1.50 (0.57)	**
Lamb traits :				
Birth weight	4.90	5.06	−0.16 (0.05)	**
8−week weight	21.05	21.55	−0.05 (0.23)	*

NS = Not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Ewe body weight

The negative genetic changes in ewe body weight when selection was for prolificacy (LLB/EJ) are not in agreement with Clarke (1972), Hanrahan (1976) and Bradford et al (1981), where they found little or no increase in mature ewe weight.

Lamb birth weight

Lamb birth weight is determined by the genotype of the foetus and the uterine environment provided by the mother, which is also partially determined by her genotype. Birth weight of lambs usually decreases with higher order birth types, and so effective selection for prolificacy, producing more multiples would be expected to reduce individual birth weights of lambs. This has been observed in the RGB selected flock. The decrease in lamb birth weight supports Owen et al (1986) in stating that within-breed selection for prolificacy could be associated with a depression of lamb birth weight. They observed a negative genetic correlation (< −1.0) between prolificacy (total lambs born per ewe lambing) and mean lamb weight at birth in Cambridge sheep.

Lamb 8-week weight

Lambs 8-week weight is an expression of their genetic potential plus dams maternal effect. Weight at this age is attained mainly by suckling dams milk. Dams maternal effect is essentially a reflection of the variation in milk supply between dams on growth of the lambs until 8-week weight. Such direct maternal effect on the young by definition, ceases at weaning (about 12 weeks of age). The negative correlated responses were consistent with the observed decline in reproductive performance when selection was for growth rate in Targhee sheep (Lasslo et al, 1985) and mice (Barria and Bradford, 1981).

The literature indicated that replication of the selected line is necessary where measuring correlated responses in any selection programme. Legates and Myers (1988) argued that even when definitely correlated responses are known to exist large populations and longer times are required to measure correlated response. However, according to Roberts (1982) a minimum of three selected lines are necessary for the interpretation of correlated responses in growth traits. The stated standard conditions were not available in the present study because the RGB would have been reluctant to finance a replicated selection scheme however desirable this may have been from a research view point.

The comparisons using an unselected control population are the most commonly used method of separating genetic and environmental changes for measuring selection response. The control group used in the present study was of the same genetic background as the selected line was. Again, since both genetic groups were maintained in the same environment the genotype-environment interaction was found to be non-existent. Therefore, the estimated correlated responses would be unbiased (Bhuiyan, 1989).

Ideally, the control line derived constant estimates should be used to obtain adjustment factors unbiased by selection. But the size of the control flock and its data set was not large enough to derive adjustment factors with small sampling errors (Bhuiyan, 1989). Therefore, the estimated correlated responses might have been slightly biased. But it could also be argued that when the data from both lines are corrected using the same adjustment factors (e.g. derived using the all data) the corrected means are likely to be treated equally and as a result, the estimation of responses should no more be erroneous (Bhuiyan, 1989).

In estimating correlated responses, genetic drift was not accounted due to lack of replicated selection lines. However, the scale of drift effect upon the phenotypic expression of traits over the generations in questions is unlikely to be significant (Falconer, 1989). Furthermore, in the control line, the lack of any positive trends in the accumulated selection differentials over the year of birth female groups would indicate that no serious genetic drift took place in this flock (Bhuiyan, 1989).

From the breeding point of view it is interesting to discuss the unilateral selection for prolificacy. If negative correlated responses are obtained for production traits (which is demonstrated here) this should mean that selection pressure should be maintained on production traits, even when considering a specialised dam-line in a crossbred scheme. This conclusion could be supported by the observed decline in ewe body weight, which through a lower milk production, could limit the growth potential of suckling lambs. Therefore in crossbred production systems, selection should be (also) on ewe body weight, and in pure bred systems, selection should presumably be on lamb birth and 8-week weights as well.

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