GENETIC CONTROL OF THE DURATION OF GESTATION IN SHEEP

G. E. BRADFORD,* R. HART,† J. F. QUIRKE‡ AND R. B. LAND

Animal Breeding Research Organization, Edinburgh EH9 3JQ

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Summary. Results of egg transfer and of reciprocal crossing among breeds of sheep with a range of 1 week in mean gestation period indicate that the genotype of the fetus is the major determinant of the duration of gestation, over a range of litter sizes from 1 to 5 and a wide range of combinations of size of donor and recipient breeds. It is concluded that the fetus accounts for at least two-thirds of the genetic variation in gestation period in this species.

Evidence for the rôle of the fetus in determining the duration of gestation comes from two independent sources, namely endocrine studies of the fetal pituitary–adrenal axis (Liggins, Kennedy & Holm, 1967; Liggins, 1969), and genetic studies, with the most critical evidence provided by interbreed egg transfer (Dickinson, Hancock, Hovell, Taylor & Wiener, 1962; Moore, 1968).

We present here the results of interbreed egg transfer and crossbreeding experiments involving breeds with a wider range of gestation periods than have been used in earlier experiments. They provide striking evidence of the rôle of the fetal genotype in determining the duration of gestation in this species.

Descriptions of the animals involved in the egg transfer experiment and of the procedures used for synchronizing oestrus in donors and recipients have been reported by Bradford, Quirke & Hart (1971). The time of onset of oestrus was recorded twice daily, and the actual time of parturition was recorded to the nearest hour, except for ewes lambing unattended during the night for which parturition was listed as occurring at 07.00 hours. The duration of gestation was calculated to the nearest half day. Where donor and recipient ewes were not exactly synchronized, the time of onset of oestrus in the donor was used as the basis for computing the gestation period; all but seven of the fifty-three recipient ewes for which gestation periods are reported were synchronized within 12 hr of the donor.

In addition to the pregnancies following egg transfer, data were obtained on seventy-seven control pregnancies, mostly of donor ewes, following intra-breed mating. The same rams, in most cases one or two per breed, were used at the oestrus from which eggs were collected and on the control group. Extensive data were also available on gestation periods from the parental flocks.

Lambs in the experiment were born during a 3-month period, March to

* Permanent address: Department of Animal Science, University of California, Davis.

† Present address: Moredun Animal Diseases Research Institute, Edinburgh.

‡ Present address: Agricultural Institute, Ballinrobe, Co. Mayo, Eire.

June, but ewes within most breed groups lambd over a much shorter period. It appeared that gestation periods later in the season were of shorter duration—an effect known in cattle (Dickinson, 1961). Gestation periods were therefore adjusted to the mean mating date, 10th December, using the pooled intra-group linear regression coefficient of duration of gestation on mating date of -0.027 days/day; the regression was negative in all nine of the groups contributing to it. The seasonal effect is undoubtedly operating at the end rather than the beginning of gestation, but the use of mating date as the independent

TABLE 1

GESTATION PERIOD OF EWES FOLLOWING THE TRANSFER OF EGGS OF VARIOUS BREEDS OF EWE TOGETHER WITH THAT OF NATURALLY MATED INTRA-BREED CONTROLS

Breed of lambs		Breed of recipient ewe			Control (intra-breed mating)	Average weight of ewe (kg)
		Finnish Landrace	Border Leicester	Welsh Mountain		
Finnish Landrace	1	142.3 $\pm$ 0.39 (8)	143.0 $\pm$ 0.69 (6)	143.2 $\pm$ 0.40 (13)	142.9 $\pm$ 0.78 (8)	51
	2	143.1 $\pm$ 0.39	143.0 $\pm$ 0.59	142.4 $\pm$ 0.39	143.7 $\pm$ 0.82	
	3				142.9 $\pm$ 0.23 (249)	
Border Leicester	3	—	—	—	145.7 $\pm$ 0.39 (31)	75
Oxford Down	1	144.6 $\pm$ 0.61 (6)	—	—	144.9 $\pm$ 0.60 (11)	89
	2	144.3 $\pm$ 0.61			145.0 $\pm$ 0.57	
	3				146.8 $\pm$ 0.75 (18)	
Southdown	1	—	—	146.2 $\pm$ 0.84 (6)	143.7 $\pm$ 0.81 (8)	50
	2			146.0 $\pm$ 0.78	144.4 $\pm$ 0.63	
	3				145.3 $\pm$ 0.25 (35)	
Welsh Mountain	1	—	—	—	146.2 $\pm$ 0.76 (7)	33
	2				146.9 $\pm$ 0.74	
	3				149.2 $\pm$ 0.26 (79)	
Soay	1	148.9 $\pm$ 0.49 (10)	—	—	148.6 $\pm$ 0.55 (11)	21
	2	148.9 $\pm$ 0.44			148.9 $\pm$ 0.53	
	3				147.9 $\pm$ 0.30 (45)	
Tasmanian Merino	1	—	150.6 $\pm$ 0.88 (4)	—	150.6 $\pm$ 0.30 (32)	42
	2		150.5 $\pm$ 0.88		149.6 $\pm$ 0.32	
	3				149.8 $\pm$ 0.27 (76)	

1: Unadjusted data. 2: Data adjusted to mean mating date (see text). 3: Intra-breed matings, previous years in the same flocks. Unadjusted data.

Gestation periods are expressed as the mean duration in days $\pm$ S.E. The number of pregnancies is given in parentheses.

variable avoids the bias towards a positive association resulting from use of lambing date.

Litter size in the experiment varied from one to five, and there are reports of an effect of litter size on gestation period (Terrill & Hazel, 1947; Forbes, 1967), but the literature is not consistent (Boshier, Martin & Quinlivan, 1969; Glimp, 1971). In the present material, the regression coefficient was negative in eight and positive in four groups, and averaged only -0.38 days over all groups for each increase of one lamb in litter size. Application of a general regression, therefore, did not appear justified and the data as presented were not adjusted for litter size.

Gestation periods of the different breeds and interbreed transfer groups are

summarized in Table 1. Values unadjusted and adjusted for lambing date are presented. These did not differ greatly; the discussion which follows is based on the adjusted values.

The results show a remarkable consistency in the duration of gestation for lambs of a given breed, regardless of the breed of ewe. In five of the six two-breed combinations, the gestation period of recipient ewes was very close to the control value for the donor breed. The sixth combination, Southdown lambs in Welsh Mountain ewes, had a mean gestation period of 146.0 ± 0.78 days, compared to 144.4 ± 0.63 days for control Southdowns and 146.9 ± 0.74 days for control Welsh Mountain ewes. The transfer lambs were thus atypically closer to the recipient than the donor mean although not significantly different from either. The mean, however, for this transfer combination (146.0 days) is closer to that of the Southdown breeding flock (145.3 days) than to that of the Welsh breeding flock (149.2 days). The weight of evidence is in favour of regarding the fetus as exerting a much stronger influence on the duration of gestation than the ewe. There was a difference of approximately 7 days in

TABLE 2
THE GESTATION PERIOD OF FINNISH LANDRACE
AND MERINO EWES CARRYING PURE OR CROSSBRED
LAMBS

	Gestation period (days)	
	Finnish Landrace ewe	Merino ewe
Finnish Landrace ram	143.1 (28)*	147.6 (22)
Merino ram	145.1 (24)	150.4 (26)

* No. of pregnancies in parentheses.

gestation period between Finnish Landrace and Merino lambs in dams of their own breeds, and the same difference when transferred to Border Leicester ewes. The ranges in actual values for the latter two transfer groups were 140.5 to 145.5, and 148.5 to 152.5 days, respectively. Moore's (1968) results of reciprocal transfer between Border Leicesters and Merinos also indicated that the genotype of the fetus determined gestation period.

An interaction between size of lamb and size of dam affecting gestation period has been reported from previous transfer experiments (Hunter, 1956; Dickinson *et al.*, 1962; Moore, 1968) such that small breed lambs in large mothers tend to have longer gestation periods, with a lesser and opposite effect for large breed lambs in small mothers. In the present experiment, any such effect was small, in spite of the wide range of sizes indicated in Table 1. Oxford Down litters in Finnish Landrace ewes had almost the same gestation period as had single-born control Oxford Down lambs. It is possible that the lengthening effect on gestation of small lamb size relative to that of the ewe is limited to litters of one; the transfer lambs in this experiment were practically all multiples.

The breeds in this experiment with the shortest and longest gestation periods, i.e. Finnish Landrace and Merino, had been crossed reciprocally over a 3-year

period in another experiment. The effects of the maternal and paternal genotype were estimated using information available within and between sheep (Patterson & Thompson, 1971). The mean values for the four lamb types are given in Table 2.

The effect of the breed of dam (i.e. difference due to maternal effects and half of genotypic effects) was 4.85 ± 0.47 days, and the sire effect (i.e. half genotypic effect) was 2.37 ± 0.43 days. The maternal effect was therefore $4.85 - 2.37$ days, i.e. 2.48 days, while breed of lamb accounted for 2×2.37 days, that is 4.74 days. Two-thirds of the variation in duration of gestation, therefore, arose from the breed of lamb, and one-third from the breed of ewe. These data are in agreement with the results of egg transfer in showing that the genotype of the fetus is more important than that of the dam, but suggest more maternal influence than do the egg transfer results. Assuming that litter size is not a significant influence, the differing results from the two sources could be due to a positive covariance between genetic effects on gestation period expressed by the fetus and by the dam, since a crossbred lamb gets half of its genes from the dam whereas a transferred lamb receives none from the ewe carrying it.

It is concluded from these results that the genotype of the fetus accounts for a high proportion of the genetic variation in gestation period, and also for a high proportion of the total phenotypic variation, over a considerable range of litter sizes and weights of donor and recipient breeds. This conclusion is in agreement with that of Prud'hon, Desvignes & Denoy (1970), who found that maternal and environmental effects accounted for less than 25% of the total variation in the duration of embryonic life in the Merino d'Arles breed. Consideration of the genotype of the lamb could, therefore, be helpful in the design of studies of the physiology of parturition, and for other purposes, such as the production of specific pathogen-free lambs, where it is necessary to anticipate the time of parturition.

As an added item of interest, we note here a case of spontaneous premature parturition from the egg transfer experiment in which viable lambs were born after 127 days' gestation. A Welsh Mountain ewe (not included in the data in Table 1) to which four Finnish Landrace embryos had been transferred was noted as ill at approximately 120 days of pregnancy and was being treated for pneumonia. On the 127th day, the ewe gave birth to three lambs, one dead but the remaining two, weighing 1.3 and 1.5 kg, were given colostrum from another ewe and were successfully raised artificially. We believe these are the first reported examples of lambs born after less than 130 days' gestation being successfully reared.

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