Ann. Rech. Vét. 1978, **9** (2), 367-374.

VARIATION IN IMMUNOGLOBULIN TRANSFER FROM EWES TO LAMBS

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Résumé

VARIATIONS DANS LE TRANSFERT DES IMMUNOGLOBULINES DE LA BREBIS A L'AGNEAU. — La teneur en IgG_1 du sérum chez des agneaux de deux jours était en corrélation significative avec la taille de la portée, la date de l'agnelage, la durée de la gestation et l'âge de la mère. Lorsque ces facteurs et quelques autres ont été compensés, on a observé des différences entre races, la concentration étant assez élevée chez la Finnoise, la Welsh Mountain et la Soay, et relativement faible chez les agneaux Border Leicester, Oxford Down et Southdown. Les concentrations des agneaux croisés étaient en rapport avec celles des races parentes. Les effets des divers facteurs étudiés sur la production de colostrum et de la quantité totale d'IgG_1 par les brebis, étaient similaires à leurs effets sur la teneur sérique en Ig des agneaux. Les productions de colostrum étaient en forte corrélation avec la production de lait. L'héritabilité de la concentration en IgG_1 chez l'agneau et de la production totale d'IgG_1 par la mère étaient estimées respectivement à 0,10 et 0,45.

Introduction

There are usually very wide variations in the concentrations of immunoglobulin obtained by young lambs from their dams during the first day after birth. This is not surprising considering the many factors that can affect immunoglobulin transfer. An increase in the amounts transferred would, no doubt, reduce the lambs' mortality rate and increase their growth rate, although probably not dramatically. The observations described here were intended to obtain more information about the reasons for the variations in transfer and to examine the possibility of improving it either by selection within breeds or by crossbreeding.

Material and Methods

Samples were collected between 1968 and 1975 from ewes and lambs on farms belonging to the Animal Breeding Research Organisation. These included two lowland farms, Dryden Mains, Roslin, Midlothian and Cold Norton, Staffordshire, an improved upland farm, Blythbank, Peeblesshire, and two hill farms, Stanhope, Peeblesshire, and Rhydyglafes, Clwyd. Details of some of these farms and the management of the sheep have been given before (Munro, 1955 ; Halliday, 1971, 1974, in press). There are meteorological stations on the farms or on adjacent farms, so comprehensive details of the weather are available.

All the ewes on Dryden Mains were taken indoors shortly before or shortly after lambing and kept there for the first few days of lactation. The Finnish × Dorset Horn ewes studied at Blythbank are under intensive management and are indoors from about a month before lambing until their lambs are weaned. All the sheep on Cold Norton, Stanhope and Rhydyglafes are outdoors throughout the year.

Colostrum samples (5 ml) were taken from both teats of most ewes, shortly after lambing and before suckling. In some cases the lambs were removed and bottle-fed, a pituitary extract was injected intravenously into the ewes (McCance, 1967) and one or both teats of each ewe milked out completely, as far as possible. The time between lambing and milking varied between 30 mins and three hours. Some ewes were also milked out from both quarters twice a day for another fortnight. Each colostrum or milk collection was weighed. Blood samples (5 ml) were taken from the ewes and their lambs into vacutainer tubes 48 hours after lambing and left at room temperature overnight before centrifugation.

The total protein concentrations in the colostrum, whey and serum samples were measured by the micro-Kjeldahl technique. The immunoglobulin concentrations were measured by the single radial diffusion method (Mancini, Carbonara and Heremans, 1965). For convenience, only the concentrations of IgG1, the principal fraction in colostrum and lamb serum, are given. The concentrations of the other important fraction, IgM, were strongly correlated with the IgG1 concentrations ($r = 0.720$, $P < 0.001$) and gave essentially the same results. Only very small amounts of IgG2 were present in the lamb serum.

There were also strong correlations between the amounts of colostrum obtained from the two teats of each ewe, and between the IgG1 concentrations in the two colostrum samples from each ewe (0.891 and 0.931, respectively, $P < 0.001$). Consequently, the mean concentration for each pair of samples was used in the analysis, and when only one teat was milked out the total yield for that ewe was estimated as twice the actual yield.

The data were analysed by the least squares and maximum likelihood general purpose programme of Harvey (1960). The effects on colostrum production and IgG1 concentrations of the year and day of lambing, the age, weight and breed of the ewe, the number, weight and sex of the lambs, the length of gestation, the total serum concentration, and other factors were calculated. The results, except in Table 1 which gives actual means, are given as least

Table 1: Details of the pure bred sheep used at Dryden Mains (means±S.E.).

Breed	No. of ewes	Ewe weights* (kg)	Gestations (days)	Mean litter size	Lamb birth weights (kg)
Oxford Down	31	95.8±2.09	146.2±0.36	1.52	5.2±0.10
Border Leicester	22	85.0±2.27	147.1±0.51	1.83	4.2±0.12
Cheviot	110	54.8±0.80	146.3±0.15	1.32	3.8±0.06
Scottish Blackface	503	53.2±0.37	145.6±0.09	1.43	3.6±0.03
Finnish Landrace	73	48.6±1.00	143.1±0.30	2.59	2.3±0.05
Southdown	62	47.4±1.04	144.7±0.24	1.45	3.3±0.07
Merino	171	42.9±0.63	150.1±0.15	1.05	3.6±0.05
Welsh	38	37.3±1.50	147.5±0.36	1.53	2.6±0.07
Shetland	35	35.6±1.71	146.9±0.32	1.69	2.8±0.11
Soay	85	21.2±1.30	148.9±0.20	1.17	2.1±0.07

* taken shortly after lambing.

Table 2: The effects of litter size on colostrum production and IgG_1 concentrations (Least squares means±S.E.).

Litter size	IgG_1 in lamb serum		Colostrum					
			Weight		Weight of IgG_1		Concentration of IgG_1	
	No.	mg/ml	No.	gms	No.	gms	No.	mg/ml
1	948	28.6±0.91	150	264.8± 32.3	150	19.6±2.31	912	89.5±2.32
2	1004	23.4±0.91	80	237.9± 33.1	80	17.6±2.36	582	95.0±2.38
3	148	17.8±1.38	11	168.9± 72.0	11	7.1±5.14	131	98.2±3.82
4	27	15.4±2.68	3	100.2±112.7	3	6.2±8.05	34	108.0±5.95
	P<0.001		NS		NS		P<0.01	

squares means or regressions, or residual correlations, after allowance has been made for other important relevant effects.

Results

Lambs on Lowland Farms

Samples were taken from 2177 lambs born on Dryden Mains between 1968 and 1975. The lambing season extended from late February to early May. Details of the larger groups of purebred sheep are given in Table 1. The IgG1 concentrations in the lambs showed significant annual variations that could not be related to the weather. The concentrations were significantly negatively correlated with litter size (Table 2), the day of lambing (Table 3), the length of gestation (— 0.319 ± 0.133 mg/day, P < 0.05), and the total serum protein concentrations of the dams (— 0.144 ± 0.057 mg/mg, P < 0.01). They were low in lambs born to very young or to old ewes (Table 4). Male lambs had higher concentrations than females but the difference was not significant.

The mean concentrations for the breeds and cross breeds are shown in Tables 5 and 6. Results from some small groups have been omitted. Among the pure breeds the concentrations were highest in Finnish, Welsh and Soay and lowest in Oxford Down, Southdown and Border Leicester lambs. In 1974 and 1975 samples were taken from 92 Oxford Down lambs at Cold Norton. Their mean concentration when adjusted for year, age and litter size (17.9 ± 0.73 mg/ml) was not significantly different from that of the Oxford Down lambs born at Dryden Mains. The concentrations in the cross breeds were more or less predictable from those in the pure breeds. The correlations between the

Table 3: Least squares regressions of colostrum production and IgG_1 concentrations on day of lambing and ewe weight.

Factors	Regression on			
	Day of lambing(1)		Weight of ewe	
	No.	per day	No.	per kg
IgG_1 concentration in lambs	2170	—0.024±0.011 mg/ml*	1760	0.034±0.037 mg/ml^{ns}
Wt. of colostrum produced	244	—1.481±0.520 gm**	244	3.720±1.786 gm*
Wt. of IgG_1 in colostrum	244	—0.106±0.037 gm**	244	0.224±0.128 gm^{ns}
IgG_1 concentration in colostrum	1661	0.062±0.021 mg/ml**	651	—0.320±0.160 mg/ml*

ns not significant; * P<0.05; ** P<0.01.
(1) January 1st=1.

Table 4: The effects of ewe age on colostrum production and IgG_1 concentrations (Least squares means±S.E.).

Ewe age (years)	IgG_1 in lamb serum		Colostrum					
			Weight		Weight of IgG_1		Concentration of IgG_1	
	No.	mg/ml	No.	gms	No.	gms	No.	mg/ml
1	100	22.6±1.45	17	118.2±71.1	17	6.2±5.08	152	98.0±5.23
2	416	24.8±1.01	32	238.2±50.0	32	13.8±3.55	542	91.9±4.77
3	477	25.5±0.99	50	161.7±43.4	50	11.1±3.10	447	88.9±4.78
4	404	24.0±0.97	64	201.2±38.6	64	14.0±2.76	212	89.8±5.06
5	343	23.6±1.03	37	203.4±47.1	37	15.5±3.37	157	92.8±5.19
6	179	21.1±1.14	44*	125.8±52.6	44*	8.6±3.54	105	98.1±5.40
7	82	21.5±1.42					36	101.4±6.72
8 or 9	99	21.9±1.45					36	100.0±6.72
		P<0.01		P<0.05		P<0.05		P<0.001

* includes 4 older ewes.

concentration for each breed or cross breed, and the mean weights of the lambs and ewes were — 0.773 and — 0.532, respectively ($P < 0.001$ and 0.01). However, the correlation between the mean concentrations and the mean total weights of lamb suckled per ewe was not significant, and the correlation between the mean concentrations and the ratios of mean weight of lamb suckled to ewe weight was strongly positive (0.547, $P < 0.01$). When breed effects were removed there were no significant effects of the weights or ratios of weights on the lambs' IgG1 concentrations.

The mortality rate between sampling and 6 months of age was 8.1 %. There were significant relationships between the IgG1 concentrations and mortality both when the mean concentration for each breed was correlated with its percentage mortality (— 0.592, $P < 0.01$) and when the mean concentration for all survivors was compared with that for all lambs which died (22.9 ± 0.88 and 18.2 ± 1.22 mg/ml, respectively, $P < 0.001$).

Lambs on Hill Farms

The lambs studied on Stanhope were from Scottish Blackface ewes which had been mated to Exmoor Horn, Swaledale, Derbyshire Gritstone, Finnish Landrace, Wensleydale, Merino or bought in Scottish Blackface rams. Those on Rhydyglafes were from Welsh, Scottish Blackface or Welsh and Scottish Blackface crossbred ewes which had been mated to Welsh or Blackface rams. They were sampled in 1975 and 1976. There were significant differences in IgG1 concentrations on both farms, the mean value being highest in Finnish crossbred lambs at Stanhope, and much higher in Welsh than in Blackface lambs at Rhydyglafes (Tables 7 and 8).

From the purebred Welsh lambs sampled on Rhydyglafes in 1975 eight ram lambs with high concentrations and eight with low concentrations (means of 49.5 ± 1.49 and 16.4 ± 2.55 mg/ml, respectively) were selected for mating with Welsh ewes in the

Table 5: IgG_1 concentrations in pure-bred lambs at Dryden Mains (Least squares means±S.E.).

Breed	No. of lambs	IgG_1 (mg/ml)
Finnish Landrace	140	31.6±1.11
Welsh Mountain	101	30.6±1.39
Soay	97	28.4±1.45
Merino	183	21.1±1.03
Scottish Blackface	780	20.7±0.65
Shetland	42	19.9±1.83
Cheviot	136	18.5±1.15
Southdown	91	15.9±1.31
Oxford Down	51	15.0±1.96
Border Leicester	42	13.0±1.93
		P<0.001

Table 6: IgG_1 concentrations in cross-bred lambs at Dryden Mains (Least squares means±S.E.).

Crosses between	No. of lambs	IgG_1 (ml/ml)
Finnish and Welsh	20	32.1±2.61
Soay and Finnish, Jacob or Mouflon	36	30.0±1.17
Finnish and Dorset Horn	44	27.8±1.96
Finnish and Blackface	107	27.0±1.34
Finnish and Merino	36	26.9±1.99
Mouflon and Merino or Wiltshire	18	24.6±1.51
Merino and Cheviot	63	24.0±1.56
Border Leicester and Finnish	19	19.0±2.70
Merino and Blackface	42	18.0±1.80
Southdown and Merino or Blackface	12	17.8±2.48
		P<0.001

Table 7: IgG_1 concentrations in lambs at Stanhope (Least squares means±S.E.).

Breed of ram*	No. of lambs	IgG_1 (mg/ml)
Finnish Landrace	42	28.8±1.63
Exmoor Horn	41	26.1±1.57
Wensleydale	26	24.8±2.00
Merino	50	23.9±1.46
Swaledale	42	22.9±1.54
North Country Cheviot	39	22.3±1.65
Derbyshire Gritstone	29	22.3±1.90
Scottish Blackface	47	22.0±1.52
		P<0.025

* all the ewes were Blackface.

Table 8: IgG_1 concentrations in lambs at Rhydyglafes (Least squares means±S.E.).

Type of lamb	No. of lambs	IgG_1 (mg/ml)
Welsh Mountain	483	33.1±1.68
Crossbred	163	30.4±1.79
Scottish Blackface	68	22.7±2.10
		P<0.001

following season. Samples were taken from 489 of their offspring born in 1976. The heritability for IgG1 concentration at 48 hours of age, based on the sire-offspring regression, was estimated at 0.10 ± 0.041 ($P < 0.05$).

Colostrum and IgG1 Production by Ewes

It was sometimes difficult to milk the ewes satisfactorily because the colostrum was very viscous, and the results probably underestimate the true amounts of IgG1 present at lambing. The very wide variations in yield also made interpretation of the results difficult. The results of the first colostrum collections from ewes at Dryden Mains are given in Tables 2, 3, 4 and 7. The relationships between the yields of colostrum or IgG1 and other factors resembled those for the lambs' serum IgG1 concentrations. The yields were low in young and old ewes, and were negatively correlated with the date of lambing and with litter size. There were also significant annual variations. There was some evidence of a positive correlation with ewe body weight.

Although the IgG1 concentration decreased with increasing interval between lambing and the first milking the total yield of IgG1 and colostrum increased (1.55 ± 0.355 and 32.3 ± 4.97 gm/hr, respectively, $P < 0.001$). When these effects were allowed for there was still a strong positive correlation between weights of colostrum and IgG1 produced ($r = 0.892$, regression = 58.7 ± 2.74 mg/gm, $P < 0.001$) and a negative correlation between the weight of colostrum produced and its IgG1 concentration (— 0.410, $P < 0.001$). The correlation between the weight and concentration of IgG1 was 0.094 ($P > 0.05$). The yield of non-immunoglobulin colostrum protein was strongly correlated with the yields both of colostrum and of IgG1 (0.925 and 0.648, respectively, $P<0.001$).

The breed differences are shown in Table 9. They show some agreement with the results from the lambs in that the IgG1 yield was highest from Finnish and lowest from Southdown ewes. However, the differences were not significant at the 5 % level. A group of 35 Scottish Blackface ewes on Stanhope gave about the same mean amount of colostrum (190.5 ± 68.5 gm) as the Scottish Blackface ewes on Dryden Mains.

The regressions of total milk production

Table 9: Weights of colostrum and IgG_1 obtained from ewes at Dryden Mains (Least squares means±S.E.).

Breed or cross	No.	Colostrum (gm)	IgG_1 (gm)
Cheviot	59	242.4±54.5	14.7±3.90
Merino	53	211.4±61.1	12.7±4.37
Finnish Landrace	30	205.9±45.3	16.6±3.24
Finnish×Dorset Horn	7	198.8±86.9	14.4±6.21
Scottish Blackface	75	196.7±50.3	12.6±3.59
Merino×Cheviot	11	191.5±69.6	11.4±4.97
Southdown	35	103.8±56.5	5.9±4.03

$0.05 < P < 0.1$.

during the first fortnight of lactation, excluding the first milking, on the total weight of IgG1 and colostrum obtained at the first milking from 56 ewes at Dryden Mains were 77.6 ± 10.62 and 5.66 ± 0.827 gm/gm, respectively ($P < 0.001$).

Colostrum was also collected from 220 Finnish × Dorset Horn ewes at Blythbank. The trends were more or less the same as at Dryden Mains and the results are not given in detail. The estimated heritability for total IgG1 production in this flock, based on half-sib analysis, was 0.45 ± 0.152 ($P. < 0.01$). Colostrum was collected twice, in successive years, from 103 ewes at Dryden Mains and Blythbank. The overall correlations between the paired results for total IgG1 and colostrum production were 0.595 and 0.546, respectively ($P < 0.001$).

IgG1 Concentrations in Colostrum

Small pre-sucking samples of colostrum were taken from large numbers of ewes on Dryden Mains, Cold Norton and Blythbank. The relationship between their IgG1 concentrations and other factors (Tables 2, 3 and 4) tended to be opposite to those of the lamb serum concentrations. The mean concentrations were higher than in the colostrum from milked-out ewes because the samples were taken sooner after lambing. They were highest in young and old ewes, positively correlated with litter size, the day of lambing and the ewe's total serum protein concentration and negatively correlated with the ewe's weight. There were significant breed differences ($P < 0.001$) but the mean concentrations were not significantly correlated with the mean serum concentrations in lambs of the same breed, although there was some tendency for the concentrations to be relatively high in Finnish and Finnish crossbred ewes. When these effects had been removed the correlation between the IgG1 concentrations in a ewe's colostrum and her lamb's serum was negligible (0.002).

Discussion

The values for total colostrum and colostrum IgG1 yield must be regarded with caution, but they have been included because of the shortage of information about colostrum production in the ewe. They are also consistent with the values for IgG1 concentration in the other colostrum samples and the lamb serum samples, which could be measured much more easily and accurately. The total yield of IgG1 increased as colostrum production increased, although the IgG1 concentration fell. Consequently, whereas the changes in total colostrum or IgG1 with changes in age of ewe, litter size, date of lambing and other factors paralleled those of the lambs' sera, the changes in the colostrum IgG1 concentrations were generally the converse of these.

Most of the effects can be readily explained. It is reasonable to expect colostrum production to be low in very young and in old ewes, and the nutritional demands of pregnant ewes carrying large litters to reduce the amounts of protein available for the colostrum. The changes in IgG1 concentrations in the colostrum and the lamb serum with increasing litter size show that the effect is much smaller than the values for total colostrum suggest. The decline in the IgG1 concentrations in the lambs can also be attributed to the greater amount of colostrum needed by large litters. The effect tended to be relatively small in breeds whose lambs had high mean concentrations. The reasons for the significant regressions on day of lambing are more obscure. It has been suggested that the appetites of the lambs may decrease as the weather gets warmer (Halliday, 1975), but this does not account for the fall in colostrum production. Possibly ewes in better condition are mated earlier. Although no relationship has yet been found, within breeds, between IgG1 transfer to lambs and the ewes' body weights, there is some evidence here that colostrum production does increase with increased body weight. The significant negative regression of the lambs' IgG1 concentrations on length of gestation is surprising, as in most groups examined previously the regression has been positive. If this is a genuine effect it could partly account for the high concentrations in Finnish lambs, which have low gestation periods. However, their concentrations were still higher than in other breeds when the effect was removed.

Evidence that the rankings of the breeds and cross breeds for mean IgG1 concentrations in the lambs is related to their genetic affinities was provided by the similarities between the two Down breeds, between some of the groups of hill lambs, and between the cross breeds and their parent breeds. It is difficult to generalise about breed differences when sheep are kept under such a wide variety of environmental conditions. It is possible, for example, that Dryden Mains is more favourable to small than to large breeds. But the results from Dryden Mains and the other farms were remarkably consistent and suggest that the breed differences may be typical. Some previous studies of Finnish, Finnish × Dorset Horn, Blackface and Merino lambs on Blythbank (Halliday, 1968 ; 1976 a ; 1976 b) gave results very similar to those described here, and a comparison between large numbers of Blackface lambs on Stanhope and Dryden Mains (Halliday, 1978) showed that, although the ewes at Stanhope had a lower standard of nutrition, and consequently, were smaller and had fewer and smaller lambs, the mean concentrations in the lambs were almost identical. The comparison between the yields of colostrum tended to confirm the similarity between the two flocks.

Of the three pure breeds whose lambs had particularly high IgG1 concentrations only the Finnish has been studied in much detail (Halliday, 1973, 1975). There was some indication here that IgG1 production is relatively high in Finnish ewes. However, egg transfer experiments have shown that Finnish lambs get higher concentrations than other lambs even when born to and suckled by ewes of other breeds. Observations of their behaviour during suckling suggested that they are exceptionally vigorous shortly after birth. But when lambs were fed pooled colostrum in amounts proportional to their body weights, to measure the efficiency of absorption across the intestine, Finnish lambs did not get significantly higher concentrations than other lambs, whereas Cheviot lambs did.

The results show that ewes producing large amounts of IgG1 in one year tend to do so also in the following year. Similar results for IgG1 transfer to the lambs have been given before (Halliday, 1975). The heritability estimates suggest that whereas IgG1 production could be improved reasonably quickly by selection within breeds, improvement in IgG1 transfer to lambs would be slow. Although IgG1 production is of very great importance in IgG1 transfer, many other factors are involved. It is possible that if the observations had been made in a more uniform environment, indoors for example, the heritability estimate would have been more encouraging. Improvement by crossbreeding is obviously possible, but its potential practical value is limited by undesirable traits, particularly as regards size, of those breeds with high rates of transfer.

In all previous experiments where reliable data were available significant positive correlations between immunoglobulin concentrations in lambs and their survival have been found. This was also true of these results. The most striking example was at Rhydyglafes where the higher IgG1 concentrations in the Welsh than in the Blackface lambs were associated with a much lower mortality rate (2.0 % and 9.4 %, respectively) between birth and weaning. The differences between the mean concentrations at 48 hours of age in lambs which die between sampling and weaning and lambs which survive are usually quite small, and the mean concentrations in a flock may be of most value as an indication of the amounts of food the lambs have obtained shortly after birth. Many lambs, particularly on hill farms, get little or no colostrum and soon die from starvation or exposure. Improvements in immunoglobulin transfer would improve the lambs' nutrition during this period as well as their disease resistance. The immunoglobulin concentrations in 48 hour old lambs are also significantly correlated with their growth rates to weaning (Halliday, 1976 a, 1978), probably because, as shown here, colostrum and IgG1 production in the ewe are both strongly correlated with milk production.

Acknowledgements

Valuable assistance in this work has been given by Mr. A. R. MacLeod and by the staff on the farms.

Summary

The IgG1 concentrations in two-day-old lambs were significantly correlated with litter size, date of lambing, length of gestation and age of the dam. When these and other effects were allowed for significant breed differences were found, the concentrations being relatively high in Finnish Landrace, Welsh Mountain and Soay lambs, and relatively low in Border Leicester, Oxford Down and Southdown lambs. The concentrations in crossbred lambs were related to those in the parent breeds. The effects of the various factors on the yields of colostrum and total IgG1 by ewes were similar to their effects on the lamb serum concentrations. The yields were highly correlated with milk production. The heritabilities for IgG1 concentration in lambs and for total IgG1 production by ewes were estimated at 0.10 and 0.45, respectively.

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