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TITLE: RELATIONSHIPS BETWEEN HEMOGLOBIN GENOTYPE AND PRODUCTION IN CROSSBRED EWES

I. REPRODUCTION AND LAMB PRODUCTION

II. WOOL AND MILK PRODUCTION AND HEALTH RELATED TRAITS

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William D. Hohenboken

I. REPRODUCTION AND LAMB PRODUCTION

Relationships among hemoglobin (Hb) genotypes and reproduction and production traits were examined in 294 four- and five-year-old North Country Cheviot, Dorset, Finnsheep or Romney x Suffolk or Columbia-type crossbred ewes. Hb BB ewe lambs were youngest at first estrus and Hb AA ewe lambs were oldest. The differences were small but consistent across crossbred groups. Ewe lamb fertility was similar for Hb AB and Hb BB ewes, and both were superior to Hb AA ewes. The difference among Hb genotypes in ewe lamb fertility, when the two Finnsheep groups (in which the Hb BB genotype was absent) were excluded, favored ewes with Hb BB over ewes with Hb AB. Results suggested heterozygote advantage in prolificacy of ewe lambs with a minor advantage of the A over the B allele. Hb BB ewes were highest, Hb AB ewes were intermediate and Hb AA ewes were lowest for average fertility over all production years. For prolificacy per ewe lambing and prolificacy per ewe exposed to mating, Hb BB ewes were superior to Hb AB and Hb AA ewes. Hb BB ewes were also superior, Hb AB ewes were intermediate and Hb AA ewes were lowest for total number

and total kg. of lambs weaned. Results suggested that the B allele enhances most traits associated with reproductive fitness. There was little suggestion of heterozygote advantage for those same characteristics.

II. WOOL AND MILK PRODUCTION AND HEALTH RELATED TRAITS

Relationships among hemoglobin (Hb) genotypes (Hb AA, Hb AB or Hb BB) and wool production, milk production and health related traits were examined in 294 North Country Cheviot, Dorset, Finnsheep or Romney, Suffolk or Columbia-type crossbred ewes. Grease wool production, staple length and side and britch fiber grades were very similar across Hb genotypes. Incidence of medullated fibers also did not differ significantly among ewes of varying Hb type. Within crossbred groups found to have some cotted fleeces, no significant difference in cotting incidence existed among Hb genotypes. Milk production, percentage milk fat and percentage milk protein also did not differ significantly among Hb genotypes. Ewes with Hb AB averaged the lowest incidence of footrot with Hb AA and Hb BB having similar scores. Ewes with Hb AA had the lowest fecal parasite egg counts while ewes with Hb AB or Hb BB were quite similar. These differences were not significant but they were reasonably consistent across crossbred groups. Ewes with Hb AA also had the lowest incidence of positive mastitis test scores with Hb BB ewes intermediate and Hb AB ewes having the highest incidence. Overdominance (as for footrot resistance) and the moderate beneficial effect of the A allele on health related traits (as for mastitis and parasite resistance) that are suggested by our findings, if real, could contribute to variation in longevity which in turn could partly explain the genetic polymorphism commonly encountered at the Hb locus in sheep.

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II. WOOL AND MILK PRODUCTION AND HEALTH RELATED TRAITS

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[1]Technical Paper No. 5221, Oregon Agricultural Experiment Station. Contribution to North Central Regional Project NC-111, Increased Efficiency of Lamb Production.

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SUMMARY

Relationships among hemoglobin (Hb) genotypes and reproduction and production traits were examined in 294 four- and five-year-old North Country Cheviot, Dorset, Finnsheep or Romney x Suffolk or Columbia-type crossbred ewes. Hb BB ewe lambs were youngest at first estrus and Hb AA ewe lambs were oldest. The differences were small but consistent across crossbred groups. Ewe lamb fertility was similar for Hb AB and Hb BB ewes, and both were superior to Hb AA ewes. The difference among Hb genotypes in ewe lamb fertility, when the two Finnsheep groups (in which the Hb BB genotype was absent) were excluded, favored ewes with Hb BB over ewes with Hb AB. Results suggested heterozygote advantage in prolificacy of ewe lambs with a minor advantage of the A over the B allele. Hb BB ewes were highest, Hb AB ewes were intermediate and Hb AA ewes were lowest for average fertility over all production years. For prolificacy per ewe lambing and prolificacy per ewe exposed to mating, Hb BB ewes were superior to Hb AB and Hb AA ewes. Hb BB ewes were also superior, Hb AB ewes were intermediate and Hb AA ewes were lowest for total number and total kg. of lambs weaned. Results suggested that the B allele enhances most traits associated with reproductive fitness. There was little suggestion of heterozygote advantage for those same characteristics.

INTRODUCTION

Since Harris and Warren (1955) demonstrated through electrophoresis of red blood cells the existence of variable hemoglobin (Hb) types in sheep, much interest has been shown in the relationship of Hb type to production and health related traits. Evans _et al_. (1956) designated the two Hb alleles as A and B; thus the three common genotypes and electrophoretic phenotypes are AA, AB, and BB. Frequencies of the Hb alleles in various breeds have been reviewed by Agar _et al_., (1972). The effect of Hb type on number of lambs born was studied by Evans and Turner (1965) and Berovides _et al_. (1977). Fertility levels of ewes with different Hb types were examined by King _et al_. (1958), Meyer _et al_. (1967) and Mayo _et al_. (1970). The relationship between age at first estrus and Hb type has not previously been studied in sheep nor has fertility of ewes lambing at one year of age. Number of lambs weaned by ewes of different Hb types was reported by Evans and Turner (1965). Little information is available on the influence of ewe Hb type on kilograms of lambs weaned per ewe, but Watson and Khattab (1964) reported that Hb AA lambs had higher gains than Hb BB lambs.

The objective of this study was to examine, within ewes of eight crossbred groups, the relationship between Hb genotype and age at first estrus, ewe lamb fertility, ewe lamb prolificacy, average annual fertility, lambs born per ewe lambing, lambs born per ewe exposed to mating, total number of lambs weaned and total kilograms of lamb weaned.

MATERIALS AND METHODS

Population and Management. The experimental population included 294 crossbred ewes from North Country Cheviot (Chev), Dorset, Finnsheep (Finn) and Romney rams mated either to grade Suffolk (Suff) or Columbia-type (Col) range ewes. They were born in 1973 and 1974. All ewes within a birth year group were managed as a single population until the end of their first breeding season (about 9 months of age). At that time, ewes were assigned at random within crossbred groups to dryland hill pasture or irrigated pasture environments, where they remained (except at lambing time) through the 1976/1977 production year. For 1977/1978, the last year for which data contributing to this experiment were collected, the two groups were merged and run on a combination of hill pasture and irrigated pasture over the course of the year. Cedillo et al. (1977) described both pre- and post-weaning management of ewe lambs, Hohenboken et al. (1976a) described the two environments and Klinger and Hohenboken (1978) outlined management procedures, calendar and disease control practices.

On August 10, 1973, and August 6, 1974, four vasectomized rams were introduced to ewe lambs born in those years. In late September of both years, the vasectomized rams were replaced by intact Hampshire rams for a 4 week mating season. Ewes were checked for raddle marks three times a week. The first recorded raddle mark was used to compute age at first estrus. Cedillo et al. (1977) described techniques and results concerning age at first estrus in greater detail.

Each year, ewes were pasture bred in September and October to Hampshire rams. Approximately four weeks prior to lambing, they were brought into a common area and were managed as a single group until after lambing. They were then returned with their lambs to the appropriate pasture environment where they remained throughout lactation. Lambs were creep fed a high concentrate pelleted ration, but ewes did not have access to supplemental feed during lactation. Lambs were weaned in June at an average age of 115 days.

Individual records were kept on all ewes. Fertility was recorded as 1 vs. 0 for success or failure to lamb, and prolificacy was recorded as number of lambs born (alive and stillborn). The only adjustment for lamb weaning weight was for lamb sex. Female weights were multiplied by 1.1 to convert them to expected male equivalent (Notter et al., 1975; Hohenboken et al., 1976b).

Blood Preparation and Electrophoresis. In September of 1978, a blood sample was collected from each of the 294 ewes. Heparinized samples were centrifuged at 2500 RPM for 10 minutes; plasma was then decanted and discarded. Blood cells were resuspended in 0.9% NaCl and centrifuged at 2500 RPM for 10 min. Samples were then decanted and the supernatants discarded. The above process was repeated three times. Following the final centrifugation, blood cells were resuspended in a volume of distilled water equal to cell mass. The samples were placed on a tube rocker for 15 minutes and then frozen. The addition of distilled water and freezing caused the cell walls to rupture, releasing cellular proteins. Samples were then thawed and centrifuged for 5 min at 1000 g. They were then diluted, 10 μl of sample to 2.5 ml distilled water, and centrifuged for 5 minutes at 1000 g. The samples could then be frozen for storage until electrophoresis could be conducted.

To prepare the sample for electrophoresis, 10 µl of tracking solution was added to 50 µl of sample, followed by thorough mixing. Ten µl of sample were then placed on top of a precast 7.5% acrylamide gel tube with a pasteur pipette. Bio-Rad Laboratories bulletin 1038 (Bio-Rad Laboratories, Richmond, Calif. 94804) describes the electrophoresis process in detail. At the completion of electrophoresis, the gels were stained by using a sigma brilliant blue R stain so that protein bands could be seen. Hemoglobin types were determined by the location of the band or bands, as in the case of Hb AB.

Statistical Analysis. Least squares analysis of variance was used to assess the relationship between Hb type and all the production traits except ewe lamb fertility and ewe lamb prolificacy. The analysis of variance included sources of variation for pasture environment, year of birth of ewe, crossbred group, Hb type, pasture x birth year, pasture x Hb type, birth year x Hb type and crossbred group x Hb type. The pasture x crossbred group and birth year x crossbred group interactions were found in preliminary analyses not to contribute significantly to variation in the dependent variables, so they were dropped from the final model. Results of the analyses of variance are summarized in table 1. Differences among pasture environments, birth years and crossbred groups are not discussed in this paper. Since ewe lamb fertility and ewe lamb prolificacy were both binomial traits (success vs. failure to reproduce and one vs. more than one lamb, respectively) χ^2 analysis was used for those two variables.

RESULTS AND DISCUSSION

Distribution of Hb types and allelic frequencies for the eight crossbred groups, for progeny of Columbia-type (Col) vs. Suffolk (Suff) ewes and for the entire population are shown in table 2. The number of Hb AA ewes was low in all groups. In only the North Country Cheviot (Chev) x Col and Finnsheep (Finn) x Col crosses were there adequate numbers of Hb AA individuals to allow meaningful within group comparisons with Hb AB and/or Hb BB ewes. In the two Finn crossbred groups, Hb BB ewes were absent, suggesting that all eight of the Finn rams siring our Finn cross ewes were Hb AA. Evans et al. (1958) reported a frequency among Finns of 1.0 for the A allele. Only four percent of Suff cross ewes were Hb AA whereas 15% of Col cross ewes were AA. In the entire population, genotypic frequencies were .095 AA, .514 AB and .391 BB, while allelic frequencies were .349 A and .651 B. Genotypic frequencies did not differ markedly from Hardy-Weinberg expectations ($P \simeq .10$), despite the fact that the population certainly wasn't mating at random. Frequency of the B allele was higher than that of the A allele in six of eight groups. B was most frequent in Dorset crosses, while A was most frequent in Finn crosses. Ewes from Suff dams had a higher frequency of B than those from Col dams.

In a large number of studies reviewed by Agar et al., (1972), within a variety of sheep populations, the B allelic frequency was generally considerably higher than that of the A allele. Stormont et al., (1968) reported that in Horned Dorset, gene frequencies were .41 and .59 for A and B, respectively, while in Columbias, allelic frequencies were .92 for B and .08 for A.

Average age at first estrus for ewes of each Hb type within each crossbred group as well as for the overall population are shown in table 3. These data represent only those ewe lambs that cycled before 1 year of age; this included 90% of the entire population and 98% and 82% of Suff cross and Col cross ewes respectively. Allelic and genotypic frequencies were similar in ewes which did vs. did not exhibit behavioral estrus by 1 year of age. Thus any trends exhibited in table 3 probably are characteristic of the entire population. Overall, Hb BB ewe lambs were youngest at first estrus with Hb AB ewes intermediate and Hb AA ewes oldest. These differences were not significant, but the trends were consistent enough within groups having adequate numbers for meaningful comparison that a small but real effect is suggested. To the best of our knowledge, the relationship between Hb type and age at first estrus in sheep has not been examined elsewhere. Gopinathan and Nair (1976), however, reported that in goats, females with Hb type AA kidded 2.5 months earlier than females of other Hb types.

Differences among Hb types in average ewe lamb fertility and ewe lamb prolificacy for the eight crossbred groups and for the entire population are also shown in table 3. The χ^2 test for ewe lamb fertility indicated that there was no significant difference among Hb types for fertility when the entire population was analyzed. However, when the two Finn cross groups (in which Hb BB was not represented) were deleted, there was a significant difference among Hb types for fertility in the remaining ewes. This difference tended to favor ewes with Hb BB over ewes with Hb AB. In four of the six groups, Hb BB ewes had higher ewe lamb fertility; in the remaining two groups, fertility of ewes with Hb BB vs. Hb AB was approximately equal. In only two groups, Chev x Col and

Finn x Col, were numbers sufficient to allow comparison of Hb AA and Hb AB ewes. In both of these cases, Hb AB conferred higher fertility than Hb AA. Thus our data support a beneficial effect of the B allele on ewe lamb fertility.

The χ^2 test for ewe lamb prolificacy indicated that in the overall population a highly significant difference existed among Hb types in ewe lambs having single vs. multiple births. When the two Finn cross groups were deleted, the χ^2 test for the remaining population remained significant but to a lesser degree. Overall, Hb type AA ewe lambs appeared to be the most prolific, but this is probably an artifact. Finn ewes (Maijala and Osterberg, 1977) and Finn crosses (Dickerson and Laster, 1975; Cedillo et al., 1977) are noted for early sexual maturity and high fertility and prolificacy when lambing at one year of age. They also have a high frequency of the A allele and the Hb AA genotype. In our study 10 of 22 Hb AA ewes were Finn crosses, and a high proportion of multiple births from ewe lambs were from the Finn cross ewes. This association does not mean, of course, that the Hb AA genotype caused the high prolificacy. Genotypic effects of Hb AA vs. Hb AB on prolificacy can be assessed fairly only in the Finn x Col and Chev x Col groups. In the latter group prolificacy was equal while in the former group, it favored Hb AA over Hb AB. Comparison of Hb AB vs. Hb BB ewes was possible in all crossbred groups except the Finn crosses. In all but one of those six groups, Hb AB ewes were as prolific or more prolific than Hb BB ewes. Our results therefore suggest a heterozygote advantage with possibly a minor advantage of the A allele over the B allele for ewe lamb prolificacy.

In table 4, average fertility for ewes of each Hb type within the eight crossbred groups as well as for the entire population is documented. Average fertility was computed over 4 or 5 years depending upon birth year of ewe. Average fertility favored Hb BB ewes with Hb AB ewes intermediate and Hb AA ewes lowest, .87, .83 and .79, respectively. Within crossbred groups, the ranking of Hb types changed considerably, as evidenced by the significant Hb type x crossbred group interaction. In the Finn cross groups, where Hb BB were not represented, Hb AB ewes had moderately higher average fertility than Hb AA ewes. In the only other group with an appreciable number of Hb AA ewes (Chev x Col), Hb AB ewes were also higher in fertility than Hb AA ewes. Only in the Chev x Col group, however, did the Hb Ab ewes have higher fertility than Hb BB ewes. Our data therefore suggest a beneficial effect of the Hb B allele on average fertility, as was suggested for ewe lamb fertility as well. Olson and Loggins (1979) also reported that among Florida native sheep, ewes with Hb BB were more fertile than ewes with Hb AA. In contradiction to these results, King et al. (1958) reported that in the Scottish Blackface breed, Hb AA ewes were more fertile than either Hb BB or Hb AB ewes, while Meyer et al. (1967) reported that among Blackheaded Mutton sheep in Germany, Hb AA ewes were more fertile than Hb BB ewes. Work done on Australian Merinos by Mayo et al. (1970) indicated no difference in fertility between Hb types.

Results for prolificacy per ewe lambing are also presented in table 4. Ewes with Hb BB were the most prolific, Hb AB ewes were intermediate and Hb AA ewes had the lowest average prolificacy -1.66, 1.55 and 1.49, respectively. In four of the six groups in which they were represented, Hb BB ewes were the most prolific. Hb AB ewes were the most prolific among the Dorset x Suff and Romney x Suff crossbred groups, with Hb BB ewes the next most prolific. Among Finn crossbreds, the Hb AA ewes were more prolific, but in all other groups Hb AA ewes had the lowest average prolificacy.

Prolificacy per ewe exposed to mating per year was also analyzed. It differed from the previous dependent variable, prolificacy per ewe lambing, in that if a ewe did not lamb, then prolificacy for that year was scored as zero. For the previous variable, if a ewe did not lamb, her record for that year did not contribute to her average prolificacy. In other words, differences among ewes in fertility contributed to differences among ewes in prolificacy per ewe exposed per year but not to differences among ewes in prolificacy per ewe lambing per year.

Average prolificacy per year for each Hb type within the eight crossbred groups and for the entire population are shown in table 4. Results were quite similar to the analysis of prolificacy per ewe lambing per year. That is, genotypes ranked fairly consistently Hb BB, Hb AB, Hb AA except that in Finn cross ewes, Hb AA conferred higher prolificacy than Hb AB. Other research (with exceptions) supports these findings that Hb BB ewes are more prolific than Hb AA or Hb AB ewes except in Finn crosses. For example, Evans and Turner (1965) reported that Hb BB Merino ewes had significantly higher lambing rates than Hb AA ewes, and Agar et al. (1972) reviewed a number of studies of various breeds in diverse environments in which the same conclusion was reached. Hanrahan et al. (1978) reported no significant difference between Hb AA and AB Finn ewes in number of ova shed but that following stimulation with PMSG, Hb AA ewes responded with higher ovulation than Hb AB ewes. Berovides (1977) reported that in Criollo sheep, Hb AA ewes were more prolific than either Hb AB or Hb BB ewes.

The average total number of lambs weaned over the entire course of the experiment per ewe of each Hb type within crossbred group is shown in table 5. Prolificacy influences number of lambs weaned as does survival percentages of the lambs. Overall, Hb BB ewes were superior, Hb AB ewes were intermediate and Hb AA ewes were lowest. In all of the crossbred groups, with the exception of the Finn crosses where they were not represented and the Romney x Col group, Hb BB ewes had the highest number of lambs weaned. In the Finn cross groups, Hb AA ewes had the higher number of lambs weaned. In the Romney x Col group, ewes with Hb AA also had the highest number of lambs weaned. Since, however, there were relatively few ewes with that genotype, this result should not be considered conclusive for the performance of a large population of Hb AA Romney x Col ewes.

Kilograms of lamb weaned per ewe is also presented in table 5. It is the best indicator of a ewe's total production. Hb BB ewes averaged 11.4 kg more lamb weaned than did Hb AB ewes and 26.7 kg more lamb weaned than Hb AA ewes. This ranking among Hb genotypes for total lamb production was quite consistent among groups with sufficient observations for meaningful comparisons.

Table 1. ANALYSES OF VARIANCE FOR GENETIC, ENVIRONMENTAL AND INTERACTION EFFECTS ON PRODUCTION TRAITS

		Mean square for:					
	df	Age at first estrus	Average fertility	Prolificacy/ year	Prolificacy/ lambing	Number of lambs weaned	Kg. of lambs weaned
Pasture environment	1	16.1	.03	.00	.00	1.3	5564.7
Year of birth of ewe	1	11616.9*	.16**	.33	.07	17.0**	35223.9*
Crossbred group	7	137.5	.07**	2.02**	1.80**	10.9**	4065.7*
Hb type	2	281.4	.05	.45*	.29	4.4	5144.7
Environment x year	1	138.4	.11	.07	.35	1.2	1916.6
Environment x Hb type	2	211.7	.24	.17	.11	2.4	1795.5
Year x Hb type	2	396.4	.07	.50	.34	5.2	6273.1*
Crossbred group x Hb type	12	224.7	.45*	.10	.11	1.0	726.9
Residual	a	404	.02	.14	.13	2.3	1720.7

[a] Residual df were 232, 265, 265, 265, 265, and 265 for the six analyses.

*P<.05 **P<.01

Table 2. Distribution of Hb types and allelic frequencies in the entire population and within crossbred groups of ewes.

	No. of animals			Gene frequency	
	AA	AB	BB	A	B
Overall	28	151	115	.349	.651
Breed					
Finn x Suff	1	27	0	.518	.482
Finn x Col	9	31	0	.612	.388
Dorset x Suff	1	5	34	.088	.912
Dorset x Col	3	12	24	.231	.769
Chev x Suff	2	21	13	.347	.653
Chev x Col	6	16	11	.424	.576
Romney x Suff	2	24	18	.318	.682
Romney x Col	4	15	15	.338	.662
Progeny of Suff dams	6	77	65	.301	.699
Progeny of Col dams	22	74	50	.404	.596

Table 3. Age at first estrus, average ewe lamb fertility and average ewe lamb prolificacy for ewes of varying Hb type, in the entire population and within crossbred groups.

	Age at first estrus			Ewe lamb fertility			Ewe lamb prolificacy		
	AA	AB	BB	AA	AB	BB	AA	AB	BB
Overall	210.5	206.3	203.5	.32	.51	.49	1.67	1.36	1.11
Breed									
Finn x Suff	203.8	204.4	-	1.00	.77	-	3.00	1.54	-
Finn x Col	208.1	209.4	-	.44	.75	-	1.75	1.57	-
Dorset x Suff	194.8	206.9	197.7	1.00	.40	.38	1.00	1.33	1.14
Dorset x Col	219.2	204.7	201.2	.00	.25	.50	-	1.33	1.17
Chev x Suff	210.8	206.5	202.8	.50	.43	.54	2.00	1.22	1.00
Chev x Col	219.8	211.2	206.1	.17	.31	.36	1.00	1.00	1.00
Romney x Suff	218.4	198.3	209.3	.00	.50	.50	-	1.00	1.00
Romney x Col	219.3	209.0	208.5	.25	.13	.20	1.00	1.00	1.33

Table 4. Average fertility, average prolificacy per ewe lambing per year and average prolificacy per ewe exposed to mating per year in the entire population and within crossbred groups.

	Average fertility			Prolificacy/lambing			Prolificacy/year		
	AA	AB	BB	AA	AB	BB	AA	AB	BB
Overall	.79	.83	.87	1.49	1.55	1.66	1.28	1.29	1.44
<u>Breed</u>									
Finn x Suff	.87	.91	-	2.23	2.13	-	2.27	1.90	-
Finn x Col	.87	.90	-	2.24	1.93	-	1.93	1.76	-
Dorset x Suff	.87	.74	.89	1.08	1.52	1.49	1.02	1.22	1.33
Dorset x Col	.43	.79	.87	1.27	1.32	1.45	.91	1.04	1.28
Chev x Suff	.94	.80	.86	1.27	1.30	1.49	1.17	1.20	1.27
Chev x Col	.77	.83	.78	1.35	1.32	1.51	1.04	1.08	1.20
Romney x Suff	.66	.84	.85	1.02	1.36	1.32	.69	1.14	1.11
Romney x Col	.88	.77	.79	1.39	1.30	1.41	1.20	1.01	1.11

Table 5. Number of lambs weaned and total kilograms of lamb weaned per ewe, in the entire population and within crossbred groups.

	Number of lambs weaned			Kilograms of lamb weaned		
	AA	AB	BB	AA	AB	BB
Overall	4.64	4.83	5.26	119.4	134.8	146.1
Breed						
Finn x Suff	6.91	6.10	-	128.2	169.8	-
Finn x Col	6.16	5.93	-	155.9	147.8	-
Dorset x Suff	3.92	5.07	5.29	120.1	143.2	161.3
Dorset x Col	3.71	4.53	4.99	88.4	123.1	143.0
Chev x Suff	4.14	4.26	4.86	132.3	123.3	133.9
Chev x Col	4.32	4.36	4.64	115.5	123.9	131.7
Romney x Suff	2.87	3.31	4.51	88.5	129.2	139.9
Romney x Col	5.09	4.04	4.19	126.6	117.8	120.3

RELATIONSHIPS BETWEEN HEMOGLOBIN GENOTYPE AND PRODUCTION IN CROSSBRED EWES
II. WOOL AND MILK PRODUCTION AND HEALTH RELATED TRAITS[1]

Martin R. Dally[2], David L. Thomas[2], William Hohenboken[2] and A. Morrie Craig[3]

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[1]Technical Paper No. 5222, Oregon Agricultural Experiment Station. Contribution to North Central Regional Project NC-111, Increased Efficiency of Lamb Production.

[2]Department of Animal Science.

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SUMMARY

Relationships among hemoglobin (Hb) genotypes (Hb AA, Hb AB or Hb BB) and wool production, milk production and health related traits were examined in 294 North Country Cheviot, Dorset, Finnsheep or Romney, Suffolk or Columbia-type crossbred ewes. Grease wool production, staple length and side and britch fiber grades were very similar across Hb genotypes. Incidence of medullated fibers also did not differ significantly among ewes of varying Hb type. Within crossbred groups found to have some cotted fleeces, no significant difference in cotting incidence existed among Hb genotypes. Milk production, percentage milk fat and percentage milk protein also did not differ significantly among Hb genotypes. Ewes with Hb AB averaged the lowest incidence of footrot with Hb AA and Hb BB having similar scores. Ewes with Hb AA had the lowest fecal parasite egg counts while ewes with Hb AB or Hb BB were quite similar. These differences were not significant but they were reasonably consistent across crossbred groups. Ewes with Hb AA also had

the lowest incidence of positive mastitis test scores with Hb BB ewes intermediate and Hb AB ewes having the highest incidence. Overdominance (as for footrot resistance) and the small beneficial effect of the A allele on health related traits (as for mastitis and parasite resistance) that are suggested by our findings, if real, could contribute to variation in longevity which in turn could partly explain the genetic polymorphism commonly encountered at the Hb locus in sheep.

INTRODUCTION

Relationships among hemoglobin type (Hb) and various wool quantity and quality traits have been examined by King _et al_. (1958), Watson and Khattab (1964), Kalla _et al_. (1971), Chopra and Chopra (1972), Aliev and Koloteva (1974), Seth _et al_. (1974), Kalla and Ghosh (1975) and Sel'kin _et al_. (1978). Although the effect of Hb type on milk production in sheep has not been studied in any great detail, Seth _et al_. (1974) reported milk production for ewes of variable Hb type in Magra ewes. Work by Huisman _et al_. (1958), which indicated that Hb AA had higher oxygen affinity than Hb BB, stimulated much interest in the effect of Hb type on disease resistance. The relationship between Hb type and resistance to internal parasites was investigated by Jilek and Bradley (1969), Altaif (1977), Altaif and Dargie (1978) and Cuperlouic _et al_., (1978). Darcel and Avery (1960) and Collis _et al_., (1977) studied the relationship between Hb type and scrapie. Resistance to footrot and mastitis as related to Hb genotype has not previously been examined.

The objectives of this study were to examine, within ewes of eight crossbred groups, the relationship between Hb genotype and fleece weight, staple length, wool grade, frequency of medullated fibers, frequency of cotting, milk production, percentage fat in milk, percentage protein in milk, mastitis incidence, footrot incidence and fecal parasite egg counts.

MATERIALS AND METHODS

Population and Management. The experimental population included 294 ewes from North Country Cheviot (Chev), Dorset, Finnsheep (Finn) and Romney rams mated either to grade Suffolk (Suff) or Columbia-type (Col) range ewes. They were born in 1973 and 1974. Ewes within each birth year and crossbred group were divided at random between irrigated and dryland hill pasture management environments, where they spent the majority of their productive lives. The population, pasture environments and management procedures were described in greater detail by Cedillo et al. (1977), Hohenboken et al. (1976a) and Klinger and Hohenboken (1978), respectively.

Data Collection. Blood sample collection and preparation and electrophoresis procedures for determining Hb genotype were described by Dally et al. (1979). Wool data were collected when ewes were approximately 13 months old and had 8 1/2 months' wool growth. Two samples, side and britch, were taken from each ewe. Samples were evaluated for staple length, fiber diameter grade (Bradford system), cotting and medullation by Wool Laboratory personnel at Montana State University, Bozeman. Individual fleece weights were recorded at shearing. Cedillo et al. (1977) described experimental procedures and results in greater detail.

Milk production and milk composition during the 1977 production year were examined on 54 ewes from the irrigated pasture group. The first milking took place approximately 1 week post partum, and ewes were then milked approximately every 2 weeks for a 15 week period. Torres-Hernandez and Hohenboken (1979) described the experiment in greater detail. Percentages of protein and fat were determined from early, mid- and late lactation samples only.

In 1976 all ewes were tested for mastitis within 24 hr after parturition using the California Mastitis Test (CMT). Footrot incidence was examined on seven occasions between spring of 1975 and spring of 1977. Scores ranged from 0 to 8 depending on the number of affected claws. The seven scores per ewe were averaged to provide estimates of individual footrot susceptability. In June of 1976, 128 ewes were selected at random within the eight crossbred groups in both pasture environments. Fecal samples were collected from each ewe approximately every 2 1/2 months during the 1976/1977 production year. Egg per gram of feces (EPG) was determined within 48 hr of sampling. Parasite susceptability as analyzed in this study was average ln(EPG+1) from six collections. Norman and Hohenboken (1979) provided greater detail on experimental procedures and results.

Statistical Analysis. Least-squares analysis of variance was used to assess the relationship between Hb genotype and all traits except wool medullation and cotting. Since these traits were binomial (presence vs. absence), χ^2 analyses were used to examine differences in incidence among Hb genotypes. The analysis of variance for wool traits included sources of variation for pasture environment, year of birth of ewe, crossbred group, Hb type, pasture x birth year, pasture x crossbred group, pasture x Hb type, birth year x crossbred group, birth year x Hb type, crossbred group x Hb type and lactation status. The pasture x birth year and pasture x crossbred group interactions were found in preliminary analyses not to contribute significantly to variation in wool traits, so they were dropped from the final model. Results of analyses of variance of wool traits are summarized in table 1.

The analyses of variance for milk production and composition included sources of variation for crossbred group, Hb type, number of lambs nursed, crossbred group x Hb type and Hb type x number of lambs nursed. Pasture environment was not a source of variation since all ewes were from irrigated pastures. Year of birth and crossbred group x number of lambs reared were omitted from the model since Torres-Hernandez and Hohenboken (1979) reported that these effects did not significantly affect milk production traits in the experiment. The analyses of variance are shown in table 2.

For health related traits, analyses of variance included sources of variation for pasture environment, birth year, crossbred group, Hb type, pasture x birth year, pasture x crossbred group, pasture x Hb type, birth year x crossbred group, birth year x Hb type and crossbred group x Hb type. Pasture x crossbred group and birth year x crossbred group interactions were dropped from the final model after preliminary analyses indicated that they did not contribute significantly to variation in the dependent variables. Results of analyses of variance for health related traits are summarized in table 3.

Differences attributable to main effects and interactions not involving Hb type will not be discussed here since they were presented by Cedillo et al. (1977), Torres-Hernandez and Hohenboken (1979) and Norman and Hohenboken (1979) for wool traits, milk production and mastitis incidence and health traits, respectively.

RESULTS AND DISCUSSION

Hb type was seldom a significant source of variation in milk, wool and health traits; likewise interactions involving Hb type seldom were important (tables 1 through 3). It is safe to conclude from these results that variation attributable to Hb genotype is small in comparison to residual variation in the traits. It is not safe to conclude that small but real differences do not exist. The structure of our population (roughly equal division of 294 ewes among eight crossbred groups with at least two of the three possible genotypes represented in each group) allowed a more detailed examination of genotypic effects than would have been possible in population of a single breed or breed cross. That is, if differences among ewes of different Hb types for production traits were consistent across groups, then real genetic differences would be suggested, despite the general lack of statistical significance of the differences. For that reason, results are examined in greater detail as follows.

Wool Traits. Least-squares means for wool traits for ewes of each Hb type within each crossbred group as well as for the entire population are presented in table 4. Ewes with Hb AA, Hb AB, and Hb BB genotypes were nearly identical in grease wool production. In addition, ranking of Hb genotypes within crossbred groups was not consistent. Our data therefore suggest no influence of Hb genotype on wool production, in disagreement with results of Sel'kin et al. (1978) that in Romney Marsh crossbred ewes the B allele is associated with higher fleece production and with results of Chopra and Chopra (1972), Aliev and Koloteva (1974) and Kalla and Ghosh (1975) with various breeds that ewes with Hb AA produce heavier fleeces. Watson and Khattab (1964) reported that within the Welsh Mountain breed, Hb AB sheep produced heavier fleeces than either Hb AA or Hb BB sheep.

Staple length was also very similar across Hb genotypes for the entire population. Within crossbred groups, rankings of Hb types changed considerably, as evidenced by the significant Hb type x crossbred group interaction. King et al. (1958) reported that in the Scottish Blackface, ewes of Hb AA produced longer staple wool than ewes with Hb BB or Hb AB. Chopra and Chopra (1972) reported similar results.

For both side and britch samples, wool grades were nearly identical for ewes of varying Hb genotype in the overall population. Within crossbred groups, difference in grade attributable to Hb genotype also were small and not consistent. Kalla et al. (1971) and Chopra and Chopra (1972), working with Chokla and Nali ewes respectively, reported that ewes with Hb AA produced finer fibers than ewes with Hb BB or Hb AB. Chopra and Chopra (1972), however, reported that in Lohi sheep, ewes of Hb AB produced finer fibers than Hb AA or Hb BB ewes.

Ewes of Hb AA had the lowest incidence of medullated fibers with Hb AB ewes intermediate and Hb BB ewes having the highest incidence - 28.6, 31.1 and 44.4% respectively. These differences were not statistically significant. Within the Dorset x Col crossbred group, however, a significant difference did exist, with a higher medullation incidence among ewes of Hb BB. Chopra and Chopra (1972) reported that in both Nali and Lohi breeds, Hb AA sheep had the lowest medullated fiber per-percentage, sheep with Hb AB were intermediate and Hb BB sheep had the highest percentage of medullated fibers. King et al. (1958) reported the opposite to be true among Scottish Blackface ewes, though differences were small and not significant.

Differences in incidence of cotting were examined within the Finn x Suff, Finn x Col and Chev x Suff groups only, since cotting was absent from all other crossbred groups. No significant differences were found to exist among Hb genotypes in the groups tested.

Milk Traits. Only one of the ewes allotted to the milk production trial had Hb AA; therefore only records of Hb AB and Hb BB ewes were analyzed. Records on Finn cross ewes (all with Hb AB) and Chev x Suff ewes (nearly all Hb AB) were analyzed and contributed to estimate of Hb main effects, but means are not presented because of insufficient numbers per genotype. Table 5 presents least-squares means for production and composition for Hb BB and Hb AB ewes within five crossbred groups and for the total population. For none of the traits were differences among Hb genotypes large overall or consistent across groups. Seth *et al*. (1974) reported that ewes with Hb BB produced more milk than ewes with Hb AA or Hb AB during a 6 week period.

Health Related Traits. Least-squares means for health related traits are presented in table 6. Ewes with Hb AB average .67 infected claws compared to .93 and .91 claws for Hb AA and Hb BB ewes. This difference was quite consistent in that in six out of the eight crossbred groups Hb AB ewes had the lowest number of infected claws. The only exceptions were lower incidence in Hb AA ewes in two groups (Chev x Suff and Romney x Suff) with few Hb AA ewes. This observed overdominance at the Hb locus for footrot resistance has not been previously reported in the literature.

Mastitis scores, as a percentage of the least-squares population mean, are presented in table 6 for ewes of each Hb genotype within each crossbred group and for the entire population. Ewes with Hb AA had the lowest incidence of positive CMT scores, Hb BB ewes were intermediate and Hb AB ewes had the highest incidence. This superiority of Hb AA ewes tended to be confirmed within crossbred groups. There was no consistent difference within groups between Hb AB and Hb BB ewes.

Least-square means for internal parasite incidence (estimated from ln(EPG+1) of fecal samples but expressed here as percentage of the overall least-squares mean) are presented in table 6. Overall, ewes with Hb AA had the lowest egg counts while ewes with Hb AB and Hb BB were quite similar. The differences were not statisitcally significant. Comparison of values within crossbred groups fails to confirm superiority of ewes with Hb AA. However, that genotype is poorly represented except among Finn x Col and Chev x Col ewes. In both those groups, Hb AA ewes are well below average in parasite eggs. Within groups as well as overall, there is little suggestion of difference between Hb AB and Hb BB ewes for parasite incidence. In agreement with our results, Jilek and Bradley (1969), Altaif (1977), Altaif and Dargie (1978) and Cuperlouic *et al*. (1978) all reported that sheep with Hb AA had higher resistance to internal parasites than sheep with Hb AB or Hb BB.

Conclusions. Our data suggest a beneficial effect of the A allele on certain health related traits. If these differences are real, if other health related traits are also affected and if these differences contribute to variation among ewes in longevity, an explanation for the genetic polymorphism at the Hb locus so commonly reported in sheep populations (Agar *et al*., 1972) is suggested. The well-documented beneficial effect of the B allele on reproduction (Agar *et al*., 1972 and Dally *et al*., 1979) combined with A superiority for longevity could create heterozygote advantage for total fitness, functional overdominance at the locus and maintenance of both alleles, at intermediate frequencies, in most populations.

Table 1. Analyses of variance for genetic, environmental and interaction effects on wool traits.

		Mean square for:			
	df	Fleece Weight	Staple Length	Side Grade	Britch Grade
Pasture environment	1	.05	3.50	35.73	98.25
Birth year	1	8.10**	4.91	8.93	210.25*
Crossbred group	7	.97**	9.25**	62.40*	76.58
Hb type	2	.06	1.36	3.96	8.47
Pasture x Hb type	2	.16	.14	15.96	41.84
Crossbred group x year	7	.92**	3.05*	166.07**	112.63**
Year x Hb type	2	.16	2.56	20.22	10.22
Crossbred group x Hb type	12	.24	3.27*	11.58	14.59
Lactation status	3	1.31**	2.66	9.83	1.97
Residual	247	.18	1.46	11.91	38.81

* P<.05
** P<.01

Table 2. Analyses of variance for genetic, environmental and interaction effects on milk production and composition.

		Mean Square for:		
	df	Milk Production	Percentage Fat	Percentage Protein
Crossbred group	7	616.8	1.79	.26*
Hb Type	1	15.1	.03	.16
Number of lambs nursed	1	1875.3	.11	.39
Crossbred group x Hb type	4	736.7	.79	.15
Hb type x number nursed	1	1747.2	1.13	.04
Residual	31	601.1	1.83	.11

* $P<.05$

Table 3. Analyses of variance for genetic, environmental and interaction effects on health related traits.

		Mean square for:		
	df	Footrot	Mastitis	ln (EPG+1)
Pasture environment	1	63.03*	.004	.99
Year of Birth of Ewe	1	2.07**	.008	1.12
Crossbred Group	7	1.06**	1.332	.34
Hb Type	2	1.14*	.652	.25
Pasture x Year	1	1.69*	1.159	.01
Pasture x Hb Type	2	1.53**	.295	.31
Year x Hb Type	2	.64	2.386	.91
Crossbred Group x Hb type	12	.49	1.269	.28
Residual	a	.28	1.247	.42

[a] Residual df were 263, 253 and 101 for three analyses.

* P<.05

** P<.01

Table 4. Least-squares means for grease fleece weight, staple length, side grade and britch grade for ewes of varying Hb type in the entire population and within crossbred groups.

	Grease Fleece Wt. (kg)			Staple Length			Side Grade			Britch Grade		
	AA	AB	BB	AA	AB	BB	AA	AB	BB	AA	AB	BB
Overall	2.1	2.1	2.2	7.67	7.50	7.65	57.5	56.0	57.1	53.2	52.6	53.3
<u>Breed</u>												
Finn x Suff	2.1	1.9	-	7.56	7.67	-	61.2	56.2	-	58.8	51.5	-
Finn x Col	2.2	2.1	-	8.61	8.73	-	58.8	58.3	-	55.8	55.4	-
Dorset x Suff	2.1	1.8	1.8	8.74	5.68	6.15	61.0	54.1	55.7	49.5	51.9	51.8
Dorset x Col	2.1	2.4	2.3	4.94	7.23	6.80	60.9	58.1	58.2	57.1	56.1	55.5
Chev x Suff	1.2	4.2	2.1	7.51	6.96	7.45	53.4	54.8	54.5	45.0	50.2	50.8
Chev x Col	2.1	2.4	2.3	7.75	7.09	7.86	58.2	57.7	58.3	55.4	52.9	54.0
Romney x Suff	2.5	2.4	2.2	6.24	8.24	8.17	50.4	54.9	54.5	49.2	50.4	51.4
Romney x Col	2.4	2.5	2.5	8.92	7.34	7.79	56.2	59.2	58.4	52.6	54.1	51.7

Table 5. Least-squares means for total milk produced, percentage of milk fat and percentage of milk protein for ewes of varying Hb type in the entire population and within crossbred groups.

	Total milk produced (L)		Percentage milk protein		Percentage milk fat	
	AB	BB	AB	BB	AB	BB
Overall	151.4	153.0	4.6	4.8	6.4	6.3
Breed						
Dorset x Suff	176.9	162.8	4.8	5.0	5.0	6.4
Dorset x Col	163.4	162.4	4.2	4.9	6.9	6.1
Chev x Col	151.9	162.1	4.3	4.2	6.7	6.0
Romney x Suff	146.6	148.6	4.9	4.7	6.0	6.3
Romney x Col	140.8	151.8	4.7	5.0	7.0	6.5

Table 6. Least-squares means for average number of footrot infected claws, ln (EPG+1) as a percentage of the mean and mastitis infection as a percentage of the mean for ewes of varying Hb types in the entire population and within crossbred group.

	Footrot			Mastitis			EPG		
	AA	AB	BB	AA	AB	BB	AA	AB	BB
Overall	.93	.67	.91	84	110	106	84	108	107
<u>Breed</u>									
Finn x Suff	1.06	.98	-	61	139	-	115	85	-
Finn x Col	1.40	.82	-	100	100	-	87	113	-
Dorset x Suff	1.06	.35	.68	35	164	101	-	113	87
Dorset x Col	1.12	.45	.66	54	112	134	58	120	121
Chev x Suff	-.37	.59	.82	159	61	80	-	106	94
Chev x Col	1.00	.75	.98	97	114	88	40	148	113
Romney x Suff	.46	.76	.78	63	104	132	77	89	134
Romney x Col	1.69	.69	.99	78	107	115	119	85	95

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