POPULATION DATA FOR THE TRANSFERRIN VARIANTS IN THE AUSTRALIAN MERINO

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[*Manuscript received March* 8, 1967]

Summary

Population data for the transferrin variants in the South Australian and Camden Park strains of the Australian Merino are reported. In all, five variants designated A, B, C, D, and E were distinguished. The relationship between these variants and those reported in previous investigations of the Merino and other breeds has been determined. In two out of the six samples there were significant departures from Hardy–Weinberg expectations. It was observed that closed flocks with small effective population size, Camden Park and one South Australian (Roseworthy) flock had fewer than five variants, the number generally found in all strains of the Australian Merino so far examined. For the Roseworthy material it was possible to demonstrate that the parent population, Anama, had the five variants. Further, the two Roseworthy flocks derived from the Anama stock had significantly different gene frequencies from that flock.

I. Introduction

Transferrin is the iron-binding protein of the blood plasma. In many species of mammals it exists in two or more genetically controlled variant forms. Ashton (1958*a*, 1958*b*) first demonstrated this to be true of sheep. Since then a number of papers have established that the Australian Merino (Ashton and Ferguson 1963), British (Khattab, Watson, and Axford 1964), Italian (Sartore 1964), Scandinavian (Efremov and Braend 1965), and several South African breeds (King and Fechter 1967) possess this polymorphism. Family data (Ashton 1958*b*; Khattab, Watson, and Axford 1964; Cooper 1966) agree with the hypothesis that the difference between the variants is controlled by multiple alleles at a single locus. To each allele there correspond two transferrin proteins, referred to collectively as a zone pair. There appear to be at least nine transferrin zone pairs, or variants, in sheep (Osterlee and Bouw 1967), distinguishable from one another by starch gel electrophoresis.

The purpose of this report is to give phenotypic and gene frequency data for various populations of the Australian Merino.

II. Materials and Methods

Transferrin typing was carried out after starch gel electrophoresis of sheep sera in the buffer system described by Ashton and Ferguson (1963) using water-cooled vertical electrophoresis trays.

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Figure 1 shows the results of starch gel electrophoresis of eight serum samples in the same discontinuous Tris citrate–lithium borate buffer system employed by Ashton and Ferguson (1963). The figure illustrates the five variants found in the Merino.

The animals sampled were from two strains of Merino: Camden Park strain and the South Australian strain (Table 1). In the description of the various flocks, the terms strain, family group, parent, and daughter studs are used in the sense given them by Short and Carter (1955) in their study of the population structure of the Australian Merino.

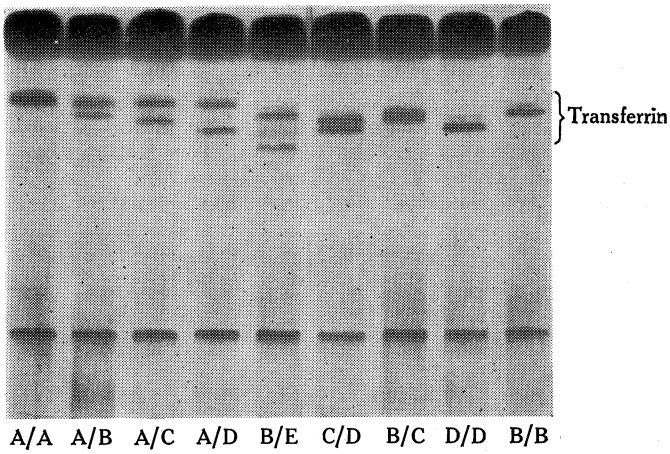

Fig. 1.—Starch gel electrophoretogram illustrating the five common variants or zone pairs (A, B, C, D, and E) distinguishable in the sera of Australian Merinos. The nine serum samples show six phenotypes from animals heterozygous at the transferrin locus (A/B, A/C, A/D, B/E, C/D, and B/C) corresponding to the genotypes Tf^{A}/Tf^{B}, Tf^{A}/Tf^{C}, Tf^{A}/Tf^{D}, Tf^{B}/Tf^{E}, Tf^{C}/Tf^{D}, and Tf^{B}/Tf^{C}) and three phenotypes from homozygotes (A/A, D/D, and B/B with corresponding genotypes Tf^{A}/Tf^{A}, Tf^{D}/Tf^{D}, Tf^{B}/Tf^{B}).

The Camden Park flock is a small flock, of about 500 sheep, closed since 1882. Its history has been given by Carter (1955). The flock is maintained only because it is thought to be descended from the earliest Merino flock in Australia, although according to Carter this is not certain. The Roseworthy Agricultural College material consists of two flocks of South Australian Merinos from the Anama parent stud; 526 ewes and 16 rams were obtained from it between 1943 and 1948, since when no further introduction has taken place (Mayo, Bradey, and Potter, unpublished data). The flock was split at random in 1953 to initiate selection experiments. One flock, the Visual flock, was selected for fleece weight by visual appraisal, while the other, the Index flock, was selected by the method of fleece weighing (Turner 1956). The animals sampled in these flocks consisted of the ewe parents of all lambs born in 1964, and some ewes culled from both flocks. One sample was taken from the Visual flock, the other from the Index flock. Each sample was sired by 25 rams over several seasons.

Mating in both flocks was at random except that matings between animals with the same sire or paternal grandparent, which ought by chance to have occurred, were completely avoided.

III. Results and Discussion

The nomenclature used is that given in Osterlee and Bouw (1967) which is now internationally accepted.

Two pairs of variants, A and G, and M and D, have very similar electrophoretic mobilities. These fine subdivisions are hard to make and were not attempted here.

Table 1

SOURCES AND NUMBERS OF SHEEP SAMPLED FOR TRANSFERRIN GROUPING

Strain	Family Group	Source	No. of Sheep Sampled
Camden Park (Macarthur Merino?)	—	F. D. McMaster Field Station, CSIRO, Badgery's Creek, N.S.W.*	32
Camden Park (Macarthur Merino?)	—	Camden Park, Camden, N.S.W.†	133
South Australian Merino	Anama	Roseworthy Agricultural College, Roseworthy, S.A.	468
South Australian Merino	Anama	Anama Stud, Brinkworth, S.A.	278
South Australian Merino (Murray Merino)	Cappeedee	One commercial flock	18
South Australian Merino	Collinsville–Ashrose	South Australian Department of Agriculture, Turretfield, S.A., and Kybybolite, S.A.	184
		One commercial flock	47
South Australian Merino	Bungaree	Commercial flocks, one daughter stud	70

* Obtained by CSIRO in 1958; bled 1962. † Bled 1964.

The original standards used were from Dr. G. C. Ashton who supplied them to one of us (D.W.C.). Standards derived from these originals have been compared with standards of Dr. J. G. Hall, Agricultural Research Council, Edinburgh, and Dr. M. Braend, Veterinary College, Oslo. The results obtained support the conclusions given in Table 2.

Table 3 shows results of testing the observed genotypic numbers against Hardy–Weinberg expectations for six samples. Two of these populations show significant departures from expectation, the first small Camden Park sample and the Roseworthy Visual flock sample. These departures are mostly due to an excess of heterozygotes.

A discussion of whether these departures are due to selective differences between genotypes, or whether they are an example of the departures from Hardy–Weinberg expectations which can occur in domestic animal populations of small effective population size, even when selection is absent (Robertson 1965), will not be entered into here. Suffice it to say that, solely on the basis of available information concerning these flocks, it is not possible to decide whether one, the other, or both are correct. The question of whether there exist genotypic selective differences is better answered

from a consideration of family data. Cooper (1967) has given a certain amount of family data which suggests that young (i.e. less than 12 months old) non-inbred animals have the expected ratio of homozygotes to heterozygotes at the transferrin locus whereas adult inbred animals have more heterozygotes than expected. This may relate to the present study; all animals were adult and, because of the closed nature of the Roseworthy and Camden Park flocks, were to a certain degree inbred. At Roseworthy it was rather slight ($F < 0{\cdot}1$) while at Camden Park, closed for a longer period, it was probably higher.

TABLE 2

RELATIONSHIP BETWEEN THE TRANSFERRIN VARIANTS OF THIS AND OTHER INVESTIGATIONS, IN ORDER OF DECREASING MOBILITY

Investigation of Osterlee and Bouw (1967)*	Investigation of Ashton and Ferguson (1963)	Investigation of Efremov and Braend (1965)	This Paper
I	—	—	—
A, G	F, G	D	A
B	A	G	B
C	H	J	C
M, D	J	M	D
E	K	P	E
P	—	—	—

* This paper reports the results of the European Society for Animal Blood Research sheep transferrin standardization trial and the internationally accepted nomenclature which arose out of the discussion of its results.

Table 4 shows gene frequencies for several strains and family groups of the Australian Merino. These data are from this and Ashton and Ferguson's (1963) investigation. Despite the rather wide variation, a consistent pattern emerges. Leaving aside the very small Murray sample, it can be said that Tf^D is always the most frequent allele. Tf^A, Tf^B, and Tf^C are widely variable, generally occupying frequencies intermediate between Tf^D on the one hand and the usually low frequency Tf^E on the other. There is considerable variation both within and between family groups.

The comparison between the Anama stud and its two daughter flocks, the Roseworthy Index and Visual, is of especial interest. The two Roseworthy flocks are homogeneous with respect to gene frequency ($\chi^2_8 = 10{\cdot}68$, $P = 0{\cdot}1$–$0{\cdot}05$) but pooled together, they are significantly different from the Anama flock ($\chi^2_5 = 13{\cdot}69$, $P = 0{\cdot}02$–$0{\cdot}01$). Furthermore, the gene Tf^C is lost from the Index flock and is at a much lower frequency in the Visual flock than in the Anama flock. Tf^E, however, is higher in frequency in the daughter flocks. Thus over the space of 17 years, approximately seven generations, substantial differences between parental and daughter populations have arisen.

There is a further feature of the gene frequency data requiring comment, namely that in the small closed flocks there are fewer alleles than in the larger ones. Camden Park has only three, Roseworthy Index only four. These two flocks have

TABLE 3

TRANSFERRIN PHENOTYPE FREQUENCIES AND HARDY–WEINBERG EXPECTATIONS FOR SIX SAMPLES

Values in parentheses indicate that classes have been pooled for χ^2 analysis because expected number in at least one class in each sample was too small

Strain		A/A	A/B	A/C	A/D	A/E	B/B	B/C	B/D	B/E	C/C	C/D	C/E	D/D	D/E	E/E	Total	χ^2	D.F.†	*P*
Collinsville–Ashrose	Obs.	3	16	11	15	0	18	22	39	0	5	14	0	22	1	0	166			
(S.A. Merino)	Exptl.	(3·47)	16·34	8·24	16·34	(0·14)	19·23	19·40	38·46	(0·34)	(4·89)	19·40	(0·17)	19·23	(0·34)	(0·00)	165·99	3·017	4	0·75–0·50
Roseworthy Index	Obs.	16	16		55	2	7		50	2				50	4	0	202			
(S.A. Merino)	Exptl.	13·64	21·31		54·32	(2·08)	8·32		42·42	(1·62)				54·06	(4·14)	(0·08)	201·99	3·609	3	0·50–0·30
Roseworthy Visual	Obs.	5	10	1	55	1	13	0	53	1	0	1	0	57	9	0	206			
(S.A. Merino)	Exptl.	7·20	16·82	(0·37)	43·36	(2·06)	9·83	(0·44)	50·68	(2·40)	(0·00)	(1·13)	(0·05)	65·32	6·19	(0·15)	206·00	11·030	3	0·02–0·01
Anama Stud	Obs.	4	23	2	57	0	11	5	68	1	0	6	0	101	0	0	278			
(S.A. Merino)	Exptl.	7·28	19·26	(2·10)	53·90	(0·16)	12·73	(2·78)	71·27	(0·21)	(0·15)	7·79	(0·02)	99·72	(0·60)	(0·00)	277·97	4·287	4	0·50–0·30
Camden Park, 1958 sample*	Obs.	1			20	4								3	3	1	32			
(Macarthur Merino)	Exptl.	5·28			11·78	(3·66)								6·57	(4·08)	(0·63)	32·00	11·160	1	0·001
Camden Park, 1964 sample*	Obs.	16			27	12								30	23	3	111			
(Macarthur Merino)	Exptl.	11·35			35·18	(13·11)								27·25	20·32	(3·79)	111·00	4·649	2	0·10–0·05

* See Table 1.

† Degrees of freedom = number of classes − number of classes pooled − number of gene frequencies calculated from the data − 1.

TABLE 4

GENE FREQUENCIES FOR TRANSFERRIN ALLELES IN VARIOUS SAMPLES FROM THE AUSTRALIAN MERINO

Sample No.	Strain	Sample	Frequency of:					Total Animals	No. of Alleles	Effective† Population Size	Years Closed
			Tf^{A}	*Tf*^{B}	*Tf*^{C}	*Tf*^{D}	*Tf*^{E}				
1	Peppin	Data of Ashton and Ferguson (1963)	0·240*	0·149	0·200	0·391	0·020	298	5	Not known	—
2	Fine Wool	Data of Ashton and Ferguson (1963)	0·012	0·314	0·279	0·371	0·024	210	5	Not known	—
3	South Australian	Commercial flocks derived from Collinsville–Ashrose	0·142	0·340	0·172	0·340	0·003	166	5	Not known	—
4	South Australian	Commercial flocks derived from the Bungaree group of studs	0·171	0·200	0·129	0·443	0·057	70	5	Not known	—
5	South Australian	Anama Stud	0·162	0·214	0·023	0·599	0·002	278	5	470	—
6	South Australian	Roseworthy Index	0·260	0·203	—	0·517	0·020	202	4	100	17
7	South Australian	Roseworthy Visual	0·187	0·218	0·005	0·563	0·027	206	5	100	17
8	South Australian	Culls from Roseworthy Index and Visual	0·292	0·167	0·008	0·533	—	60	4	100	17
9	South Australian	Murray	—	0·694	—	0·306	—	18	2	Not known	110
10	Camden Park	Camden Park	0·339	—	—	0·486	0·175	143	3	Not known	80

* Pooling *Tf*^{A} and *Tf*^{G}. † After Wright (1931).

a small effective population size. This suggests that small effective population size results in, or at least partly expedites, a loss of alleles. Loss has demonstrably occurred in the case of the Roseworthy Index flock and it seems a reasonable explanation for the Camden Park flock. It is unlikely that this latter flock would have started without these alleles. Selection could also have operated to remove them but the small population size is the *sine qua non* of their rapid removal.

Results such as this could have been predicted upon the basis of general theory of the maintenance of variability in small closed populations (e.g. Kimura 1955; Robertson 1962). However, this is one of the few cases where the fact of the loss has actually been documented by reference to the original parental population. The result for the Camden Park flock is an interesting comment upon an attempt to preserve a domestic animal in its original unimproved form. Obviously a larger population size is needed to avoid genetic drift, particularly at loci with multiple alleles.

IV. Acknowledgments

We are greatly indebted to Mr. R. H. Hayman for his hospitality and help during the course of collecting the Camden Park samples. We are also most thankful to Mr. J. Hawker, proprietor of Anama Stud, and to Mr. C. Bungey, Roseworthy Agricultural College, for their hospitality and for allowing us access to their animals and records. One of us (D.W.C.) wishes to acknowledge the assistance of a Wool Research Fellowship during the course of this study; one of us (L.F.B.), an Australian Dairy Produce Board Senior Post-graduate Studentship; and one of us (O.M.), a Commonwealth Post-graduate Award.

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