INTERRELATIONSHIPS OF ERYTHROCYTE CHARACTERS AND OTHER CHARACTERS OF BRITISH AND ZEBU CROSSBRED BEEF CATTLE

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Summary

The following red cell characters were studied in a herd of 217 calves representing Brahman cross, Africander cross, Grade Brahman, and British (Hereford × Shorthorn) breeding, and in their dams: packed cell volume, haemoglobin level, red cell count, fragility, potassium and sodium concentrations, catalase activity, and haemoglobin type. There were distinct breed differences. In some characters, e.g. packed cell volume and potassium concentration, Africander cross were intermediate between Brahman cross and British, whereas in others, e.g. fragility and catalase activity, they were indistinguishable from British. Within breeds, the characters showed highly repeatable differences between animals and high heritabilities.

Haemoglobin type was associated with differences in packed cell volume, haemoglobin level, red cell count, fragility, and potassium concentration, and there was evidence of linkage between haemoglobin type and catalase activity. Fragility, potassium concentration, and catalase activity were not correlated with each other and are independent characters each under strong genetic control.

There was evidence that low red cell count (or packed cell volume or haemoglobin level) and high fragility and high potassium level are unfavourable characters, but none showed strong predictive value for growth rate or other indices of adaptation.

I. Introduction

Evans (1963) found Zebus and Zebu crossbreds had higher packed cell volumes, erythrocyte sodium concentrations, and gene frequencies for fast-moving haemoglobin, and had lower erythrocyte potassium concentrations and corpuscular fragilities than British breeds. He pointed out that if the breeds he used were ranked according to these blood characters, the ranking was the same as that for a number of indices of adaptability to tropical environments, and suggested that these correlations might signify that erythrocyte characters are indices of tropical adaptation.

An observation that several breed groups are ranked in the same order for two characters is of course only suggestive evidence of an important functional correlation between the characters. This applies to relationships between erythrocyte characters and between these characters and measures of adaptation. In this paper, these relationships are more critically tested in terms of correlations between individual animals within breed groups.

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II. Materials and Methods

Evans (1963) reported breed means for data collected from about 550 breeding cows and bulls bled in February 1959. In this paper, the main data are from progeny of these cows, born in October–December 1959, and bled in February 1961 and again in August 1961. There were 265 calves but data are presented only from the 217 calves on which the measurements made in each month were complete. There were 178 dam–calf pairs from which complete data were available, and these have been used for estimates of heritability.

The calves included both steers and heifers and were crossbreds of the following nature:

Grade Brahman: At least seven-eighths Brahman, graded up over several generations from nondescript Brahman-cross cows. Means for this group are presented but no correlations or heritabilities are given.

Brahman Cross: Half Brahman, half British. They include both F_1 and F_2 generations, the F_1 being progeny by Brahman bulls out of Hereford or Shorthorn cows, the F_2 progeny of *inter-se* matings of F_1, e.g. Brahman–Shorthorn × Brahman–Shorthorn.

Africander Cross: Half Africander, half British; F_1 and F_2 generations in the same manner as Brahman cross.

British: Reciprocal crosses of reciprocal crosses of Herefords and Shorthorns.

All these animals were run together as a herd throughout their growing life, at the National Cattle Breeding Station, Belmont, Rockhampton (Kennedy and Turner 1959).

Table 1 shows the determinations made on red cells, the samplings to which they were applied, the methods used, and the units of measurement. Note that the nomenclature used for haemoglobin types follows established usage (Cabannes and Serain 1955; Bangham 1957; Bangham and Blumberg 1958; Crockett, Koger, and Chapman 1963) and that this is the opposite of the established nomenclature for the analogous sheep haemoglobins.

Besides these red cell characters, the following information on the same animals was used in analyses: plasma protein-bound iodine determinations which have been reported by Post (1963); mean coat score of the calves as yearlings (Turner and Schleger 1960); rectal temperature measured in November 1960; birth weight; body weight at 2 years of age in October 1961; summer gain, being gain in body weight from weaning in August 1960 to March 1961; winter gain, from March 1961 to October 1961; β-globulin (transferrin) typings provided by Dr. G. C. Ashton.

The following data on the dam of each calf were used: packed cell volume, red cell potassium and sodium concentrations, median corpuscular fragility, and catalase activity. Catalase activity for cows was measured by a slightly different method (adapted from Barton 1949) from that used for calves and was expressed as arbitrary units per unit of packed cell volume. These data on dams were obtained in February 1959 and correspond to those reported by Evans (1963).

All characters of calves and dams were subjected to statistical analysis by computer, which provided the correlation of each character with every other character. The analyses were done on three groups of measurements separately, viz. those of British, F_1 Zebu-cross, and F_2 Zebu-cross calves. The effect of breed, sex, haemoglobin type, and age of calf were progressively removed, and the correlations reported here are those pertaining when these effects are removed.

Use is made of supplementary results from 10 steers (four Brahman × Shorthorn F_2, six Hereford × Shorthorn) born in 1960 and sampled twice at an interval of 1 week when 2 years old.

Table 1

RED CELL CHARACTERS DETERMINED ON CALVES

Determination (units in parenthesis)	Sampled Feb. 1961	Sampled Aug. 1961	Method	Comment
Packed cell volume (%)	+	+	Microhaematocrit	10,000 *g* for 4 min
Haemoglobin concentration (g/100 ml)	+	+	Oxyhaemoglobin: Shimadzu spectrophotometer	
Red cell count (millions/mm^3)		+	Haemascope	Turbidimetric, incorporating compensation for cell size
Mean corpuscular haemoglobin concentration (g/100 ml)	+	+	Calculation	Haemoglobin/packed cell volume
Mean corpuscular haemoglobin (pg)		+	Calculation	Haemoglobin/red cell count
Mean corpuscular volume (μ^3)		+	Calculation	Packed cell volume/red cell count
Erythrocyte potassium concentration (m-equiv/l)	+		EEL flame photometer	By calculation, using whole blood and plasma concentrations, and packed cell volume
Erythrocyte sodium concentration (m-equiv/l)	+		EEL flame photometer	By calculation, using whole blood and plasma concentrations, and packed cell volume
Median corpuscular fragility (mg NaCl/100 ml)	+	+	Ponder (1948)	
Catalase activity (μl O_2/10 mg haemoglobin)	+	+	Miller (1958)	
Haemoglobin type	+		Evans (1963)	Slow-running type=A Fast-running type=B

III. Results

(a) *Breed Group Means*

Mean values of red cell characters are shown in Table 2. The six breed groups are arranged in descending order of apparent adaptation to a subtropical environment, viz. Grade Brahman, F_1 Brahman cross, F_2 Brahman cross, F_1 Africander cross, F_2 Africander cross, and British. This ranking is indicated by body weights of the breeds with the exception of the Grade Brahmans which are inferior in growth rates to crossbreds, but are very tolerant of tropical stresses. In the table they appear to be more inferior than they really are since they were 3 months younger at weighing.

The results confirm and extend those reported by Evans (1963). Packed cell volume, haemoglobin, and red cell count decreased significantly from Grade Brahman

TABLE 2

MEAN VALUES* OF RED CELL CHARACTERS FOR BREED GROUPS

Standard errors in parenthesis

Character	Grade Brahman	Brahman Cross		Africander Cross		British
		F_1	F_2	F_1	F_2	
Number of animals	12	27	26	78	42	32
Body weight (lb)†	508	655	629	572	531	486
	(20)	(11)	(12)	(6)	(8)	(11)
Packed cell volume						
February	42·4	39·2	34·9	31·5	28·9	27·9
	(1·6)	(1·0)	(1·0)	(0·5)	(0·5)	(0·7)
August	38·5	38·5	36·2	34·2	32·7	30·6
	(1·2)	(0·7)	(0·8)	(0·4)	(0·5)	(0·6)
Haemoglobin						
February	14·5	14·1	12·4	11·9	11·3	10·9
	(0·5)	(0·3)	(0·3)	(0·2)	(0·3)	(0·2)
August	14·0	14·4	13·4	12·9	12·5	11·3
	(0·5)	(0·2)	(0·2)	(0·2)	(0·2)	(0·2)
Red cell count, August	6·93	6·29	5·89	5·70	5·42	4·96
	(0·32)	(0·14)	(0·14)	(0·08)	(0·10)	(0·10)
Mean corpuscular haemoglobin concn., August	36·3	37·4	37·2	37·8	38·3	36·9
	(1·3)	(0·6)	(0·6)	(0·5)	(0·5)	(0·7)
Mean corpuscular volume, August	56·0	61·4	61·7	60·1	60·4	61·9
	(1·3)	(0·7)	(1·1)	(0·5)	(0·8)	(1·0)
Mean corpuscular haemoglobin, August	20·2	22·9	22·8	22·6	23·1	22·7
	(0·8)	(0·4)	(0·4)	(0·3)	(0·4)	(0·5)
Erythrocyte potassium concn., February	12·4	15·1	16·2	18·5	20·1	20·5
	(0·7)	(0·5)	(0·6)	(0·4)	(0·7)	(0·6)
Erythrocyte sodium concn., February	87·0	77·3	73·7	75·0	77·8	74·4
	(1·6)	(2·3)	(2·2)	(2·1)	(1·9)	(2·8)
Mean corpuscular fragility						
February	510	510	516	562	564	561
	(11)	(5)	(7)	(3)	(4)	(5)
August	497	528	511	574	574	573
	(6)	(5)	(6)	(2)	(3)	(3)
Catalase activity						
February	63·0	75·6	69·0	85·7	86·6	83·0
	(5·0)	(2·2)	(3·7)	(1·5)	(2·2)	(1·6)
August	76·5	75·1	67·4	87·7	95·7	79·9
	(5·8)	(2·4)	(3·5)	(1·5)	(2·1)	(1·9)

* For units of measurement, see Table 1.

† Two years old except Grade Brahmans which were 3 months younger.

through Brahman cross and Africander cross to British, values for British being about 75% of those for Grade Brahman. Mean corpuscular volume was significantly lower

TABLE 3

MEAN VALUES OF RED CELL CHARACTERS FOR CALVES OF HAEMOGLOBIN TYPE AB AND AA

Character	Grade Brahman		Brahman Cross				Africander Cross				P†
			F_1		F_2		F_1		F_2		
Haemoglobin type	AB	AA	AB	AA	AB	AA	AB	AA	AB	AA	
No. of animals	6	5	8	19	4	22	11	67	3	39	
Packed cell volume*	40·0	42·2	39·1	38·7	33·6	35·9	30·1	33·3	28·0	31·1	<0·05
Haemoglobin*	13·9	15·1	14·1	14·4	12·3	13·1	11·2	12·7	10·6	12·0	<0·01
Red cell count	6·96	7·08	6·31	6·29	5·75	5·91	5·22	5·78	5·20	5·43	<0·05
Mean corpuscular volume	55·0	56·6	61·4	61·4	61·3	61·8	62·6	59·7	57·7	60·6	
Mean corpuscular haemoglobin concn.	35·8	37·1	36·7	37·7	37·2	37·2	36·0	38·1	37·8	38·3	<0·05
Erythrocyte potassium concn.	12·6	11·3	15·6	15·0	20·1	15·5	19·8	18·2	21·7	20·0	<0·05
Erythrocyte sodium concn.	89	84	78	77	70	74	72	75	72	78	
Mean corpuscular fragility*	518	493	534	513	524	512	587	565	583	568	<0·01
Catalase activity*	69	69	78	74	61	70	71	89	86	92	
Body weight (lb)‡	476	524	669	649	626	629	568	572	499	533	

* Mean of February and August values. † Significance of weighted mean difference between haemoglobin types (Snedecor 1956).

‡ Two years old.

in Grade Brahmans but similar in the other groups. Mean corpuscular haemoglobin also was low in Grade Brahmans. There was no constant trend in mean corpuscular haemoglobin concentration. Red cell potassium concentration rose markedly through the breed groups; the converse variation in red cell sodium was less consistent. Levels of median corpuscular fragility fell into two groups which differed markedly from each other. Grade Brahman and Brahman cross animals scored about 510, whereas Africander cross and British both scored about 565. Likewise all groups with Brahman blood were much lower in catalase activity than the Africander cross or British but there was no consistent pattern of difference between subgroups within these two groupings.

Steers and heifers did not differ significantly in any of these red cell characters.

The frequency of the gene for type B haemoglobin was zero in British breed calves, 0·06 in Africander cross, and 0·13 in Brahman cross.

(b) *Differences Associated with Haemoglobin Type*

Only two animals, one Grade Brahman and one pure-bred Brahman, were found homozygous for type B haemoglobin. These comparisons are therefore between heterozygotes and type A homozygotes. Mean values of various characters of red cells from the animals of each type are shown in Table 3. The heterozygotes were lower in packed cell volume, haemoglobin level, and red cell count, and higher in median corpuscular fragility. They did not differ significantly in mean corpuscular volume but were lower in mean corpuscular haemoglobin concentration. Red cell potassium concentration was higher in heterozygotes.

In catalase activity, heterozygotes tended to be lower than homozygotes. However, the comparison is variable in different groups, and the data have been broken down to check the comparison within progeny groups of individual sires. The results in Table 4 include data for cows (sampled 1959) as well as for calves (sampled twice in 1961). The catalase values for cows and calves are on different scales of measurement and are not directly comparable. All progeny groups shown were out of British breed (haemoglobin type AA) cows with the exception of the four groups of F_2 calves by Zebu-cross bulls; in these groups all four sires were type AA but the Zebu-cross dams included some AB as well as AA animals.

All progeny groups, including those by type AA Brahman and Africander sires and those by British breed sires, are shown in Table 4. In general, Africander cross and British breed animals were similar in catalase activity, whereas Brahman cross were at a lower level. Apart from this breed difference, there were significant differences between progeny groups.

In two progeny groups by AB sires (Africander 4 and Brahman 2), AB progeny were significantly lower in catalase than AA. In another group (Africander 2), although numbers were adequate to show a difference if it existed, AA and AB progeny were practically identical in catalase activity. In a further group (Brahman 4 calves), catalase was significantly *higher* in AB than in AA calves. Thus catalase activity may be lower, the same, or higher in AB in comparison with AA animals, depending on the progeny group. There is one slight anomaly in that the cow progeny of Brahman 4 did not show the contrast shown by the same sire's calf progeny, but there were only six (three AA, three AB) cow progeny.

TABLE 4

CATALASE ACTIVITY OF PROGENY OF INDIVIDUAL SIRES, ACCORDING TO HAEMOGLOBIN TYPE OF PROGENY

Asterisks denote significance of difference in catalase activity between AA and AB calves by the same sire

Sire	Type of Sire	Haemoglobin Type: AA			Haemoglobin Type: AB		
		No.	Mean	S.E.	No.	Mean	S.E.
			Calf Data				
Brahman 4	AB	7	64·7	1·4	4	80·3***	1·9
5	AA	4	84·3	4·3			
6	AB	8	76·4	4·0	3	71·0	6·5
Brahman × Hereford	AA	16	74·4	2·9	3	70·0	6·7
Brahman × Shorthorn	AA	8	64·1	7·6	3	49·0	1·0
Africander 1	AA	14	87·5	1·7			
3	AA	17	89·1	1·8			
4	AB	9	86·4	3·9	11	70·5**	3·5
5	AA	9	88·7	3·5			
7	AA	18	94·4	2·5			
Africander × Hereford	AA	19	87·7	2·4	2	89·0	7·5
Africander × Shorthorn	AA	21	92·7	2·1	2	79·0	6·7
Hereford × Shorthorn 1	AA	17	78·9	1·9			
Shorthorn × Hereford 2	AA	15	84·6	1·9			
			Cow Data				
Brahman 1	AA	22	18·1	1·6			
2	AB	20	23·9	1·3	13	18·3*	1·6
4	AB	3	23·3	2·3	3	21·9	1·9
Africander 1	AA	21	22·4	1·3			
2	AB	8	21·4	1·5	15	20·1	1·1
3	AA	17	27·9	1·9			
M	AA	14	26·4	1·9			
Hereford 1	AA	14	26·4	1·7			
2	AA	30	26·2	1·2			
3	AA	14	27·1	1·7			
4	AA	2	26·6	4·5			
5	AA	11	28·2	1·9			
N	AA	30	22·8	1·2			
S	AA	12	27·9	1·8			
Shorthorn 1	AA	8	25·5	2·2			
2	AA	18	26·5	1·5			
3	AA	20	23·8	1·4			
4	AA	9	23·8	2·1			

* $P < 0 \cdot 05$. ** $P < 0 \cdot 01$. *** $P < 0 \cdot 001$.

It appears that part at least of the genetic control of catalase activity segregates in a simple manner and this is associated with segregation of haemoglobin type, but catalase activity and haemoglobin type are not consistently correlated. Further evidence of segregation, independent of haemoglobin type, is reflected by the high standard error of catalase activity in the F_2 Brahman × Shorthorn calves (Table 4). The values for individual calves by this sire were: type AB, 47, 50, 50; type AA, 32, 45, 48, 48, 55, 73, 78, 88, 91. Eight values (mean 47) lie clearly below the general levels for calves in Table 4, whereas the remaining four (mean 83) are typical of the higher values for Brahman progeny groups.

In view of the variable association between catalase activity and haemoglobin type, depending on pedigree, and particularly the marked reversal of association in the calves of Brahman 4, the other parameters shown to vary with haemoglobin type (Table 3) have been checked in this progeny group. The group is consistent with

Table 5

CORRELATIONS BETWEEN FEBRUARY AND AUGUST VALUES OF RED CELL CHARACTERS AND BETWEEN DAM AND CALF VALUES WITHIN BREED, SEX, AND HAEMOGLOBIN TYPE

Red Cell Character	British	F_2	F_1
		Repeatabilities	
Degrees of freedom	25	48	95
Packed cell volume	0·428*	0·424**	0·533**
Haemoglobin	0·389*	0·481**	0·595**
Mean corpuscular haemoglobin concn.	0·151	−0·103	0·052
Mean corpuscular fragility	0·529**	0·753**	0·577**
Catalase activity	0·225	0·571**	0·523**
		Dam–Calf Correlations	
Degrees of freedom	24	48	78
Packed cell volume	−0·279	0·263	0·243*
Mean corpuscular fragility	0·402*	0·324*	0·291**
Catalase activity	0·216	0·296*	0·127
Erythrocyte potassium concn.	0·377	0·371**	0·232
Erythrocyte sodium concn.	0·146	−0·133	−0·140

$*P < 0{\cdot}05$. $**P < 0{\cdot}01$.

others, however, in the effects of haemoglobin type on packed cell volume, haemoglobin level, red cell count, mean corpuscular haemoglobin concentration, and fragility, so these characteristics are associated with haemoglobin type, not with catalase activity.

One possible exception to consistent relationship with haemoglobin type is two-year-old body weight. Within sexes, there is a tendency for AB calves to be lighter than AA in some of the F_2 groups, and in the Grade Brahmans this is highly significant (difference = 59 lb, $F_{1,\,8} = 18{\cdot}9$). In the progeny groups of Africander 4 and Brahman 6 there is no significant difference, but the AB progeny of Brahman 4 were significantly heavier than his AA calves (difference = 50 lb, $F_{1,\,8} = 7{\cdot}03$). This is a similar reversal to that with catalase.

(c) *Repeatability and Heritability of Red Cell Characters*

Correlations between determinations for samples taken from calves in February and August, and correlations between values for dams and mean values for their calves are shown in Table 5. The correlations were calculated after removing effects of breed, sex, haemoglobin type, and age of calves. Sire groups were not taken into account and this may have reduced dam–calf correlations. Correlations are shown separately for British, F_1, and F_2 calves. Heritabilities may be estimated as twice the dam–calf correlations, but should be understood as applying to these particular populations, in which the F_1 data refer to Zebu-cross calves out of British dams, and the F_2 to Zebu-cross calves out of Zebu-cross dams.

The highly significant repeatabilities show that there are quite consistent differences between individual animals in packed cell volume, haemoglobin level, fragility, and, despite removal of some major differences associated with haemoglobin type, also in catalase activity. Mean corpuscular haemoglobin concentration showed zero repeatability.

TABLE 6

RED CELL CHARACTERS OF 10 STEERS AT TWO SAMPLINGS, 1 WEEK APART

Red Cell Character	Day 1†	Day 8†	Difference	Repeatability
Packed cell volume	42·3	40·4	1·9**	0·839**
Haemoglobin	15·6	14·7	0·9**	0·890**
Red cell count	6·73	6·71	0·02	0·925**
Mean corpuscular haemoglobin concn.	36·8	36·3	0·5	0·305
Mean corpuscular volume	63·5	60·8	2·7*	0·854**
Mean corpuscular haemoglobin	23·3	22·1	1·3*	0·809**
Mean corpuscular fragility	516	511	6**	0·995**
Erythrocyte potassium concn.	20·9	21·5	0·6	0·919**
Correlations between Characters	**Between Animals‡**		**Interaction§**	
Haemoglobin and packed cell volume	0·995**		0·863**	
Haemoglobin and red cell count	0·837**		0·284	
Packed cell volume and red cell count	0·830**		0·373	

* $P < 0·05$. ** $P < 0·01$. † Mean values.

‡ Using animal components of variance and covariance.

§ From animals × days interactions.

These results are supplemented by data on 10 Brahman × Shorthorn and Hereford × Shorthorn steers sampled at an interval of 1 week. Repeatabilities of various characters are shown in the last column of the first part of Table 6. Noteworthy are the high repeatability of red cell count, the absence again of significant repeatability in mean corpuscular haemoglobin concentration, and the existence of highly consistent differences between animals in mean corpuscular volume and corpuscular haemoglobin. In addition, these animals provided evidence of particularly high levels of repeatability for median corpuscular fragility (0·995 overall, 0·983 within breeds) and red cell potassium concentration (0·919 overall, 0·826 within breeds).

As strong maternal effects on erythrocyte characters are not probable, the dam–calf correlations (Table 5) indicate a large genetic component in animal differences. As results for the different generation groups differ only little, mean heritabilities of 0·34 for packed cell volume, 0·64 for fragility, 0·59 for red cell potassium concentration, and 0 for red cell sodium concentration may be estimated. The estimate of 0·37 for catalase activity, calculated as it is within haemoglobin types and across sire groups, is inadequate in view of the evidence of major gene effects shown in the previous section, but is still highly significant.

(*d*) *Relationships between Red Cell Characters*

Relationships between haemoglobin type and other characters were presented in Section III(*b*).

Very high correlations found between packed cell volume, haemoglobin, and red cell count are axiomatic. However, they do differ significantly as follows: packed cell volume and haemoglobin, 0·854; packed cell volume and count, 0·740; haemoglobin and count, 0·827. Packed cell volume and haemoglobin were closely associated but varied to some extent independently of count; this close association is reflected in the lack of repeatable variation in their ratio, namely, mean corpuscular haemoglobin concentration (Tables 5 and 6).

Relationships between packed cell volume, haemoglobin, and red cell count are shown more fully by determinations that were made on two samples taken at an interval of 1 week from 10 steers (Table 6). During the week both packed cell volume and haemoglobin fell significantly so that mean corpuscular haemoglobin concentration did not change. Mean red cell count was remarkably constant as also were the values for individual animals, shown by the high repeatability (0·925) of count. Mean corpuscular volume and mean corpuscular haemoglobin fell significantly. Packed cell volume and haemoglobin were very closely correlated whether their variations arose from differences between animals or from animals × days interaction. By contrast, while red cell count was fairly closely correlated with packed cell volume and haemoglobin in comparisons of mean values for individual animals, these correlations were absent when changes in the values for individual animals from one day to the other were considered. In view of the high repeatabilities, these phenomena clearly do not arise from errors of determination. They indicate that, while values of red cell count for individual animals remained constant, mean corpuscular volume and mean corpuscular haemoglobin fell together, but to differing degrees in different animals.

In view of this evidence favouring red cell count over packed cell volume and haemoglobin as a more stable animal character, it is chosen as representative in the correlations with other characters, shown in Table 7. In this table, the correlations between various red cell characters, calculated between animals, within breed, sex, and haemoglobin type, are given. Alongside are shown the relationships indicated by breed differences and by differences in haemoglobin type.

Four sets of correlations are clearly significant. Some must be viewed with caution, when they refer to characters derived by calculation from common factors. The evidence of higher fragility in animals with small cells ($r = -0{\cdot}314$) is uncomplicated. The size of the correlation between high cell number and small cell size ($r = -0{\cdot}475$) and evidence from related correlations indicate that this association is real, not an artefact of common errors. The inverse correlation between mean corpuscular haemoglobin concentration (haemoglobin/packed cell volume) and mean corpuscular volume (packed cell volume/red cell count) ($r = -0{\cdot}510$) arises from the fact that count is more strongly correlated with haemoglobin than with packed

TABLE 7

CORRELATIONS BETWEEN RED CELL CHARACTERS AMONG ANIMALS OF SAME BREED, SEX, AND HAEMOGLOBIN TYPE, TOGETHER WITH NATURE OF RELATIONSHIPS FOUND BETWEEN BREEDS AND BETWEEN HAEMOGLOBIN TYPES

	British	F_2	F_1	Brahman *v.* British§	Haemoglobin Type AA *v.* Type AB§
Degrees of freedom	25	48	95	0	0
Red cell count and:					
Mean corpuscular haemoglobin concn.†	0·260	0·005	−0·129	0	+
Mean corpuscular volume	−0·444*	−0·541**	−0·449**	−	0
Mean corpuscular fragility†	0·074	0·194	0·186	−	−
Erythrocyte potassium concn.	0·193	−0·113	−0·002	−	−
Erythrocyte sodium concn.	0·413*	0·361*	0·206*	+	+
Catalase activity†	−0·110	0·084	0·009	−	±
Mean corpuscular haemoglobin concn. and:					
Mean corpuscular volume‡	−0·836**	−0·218	−0·500**	0	0
Mean corpuscular fragility	0·196	0·092	0·003	0	−
Erythrocyte potassium concn.	0·112	0·093	0·139	0	−
Erythrocyte sodium concn.	0·068	0·027	0·026	0	+
Catalase activity	−0·194	−0·151	0·071	0	±
Mean corpuscular volume and:					
Mean corpuscular fragility	−0·396*	−0·350*	−0·254*	+	0
Erythrocyte potassium concn.	0·249	0·195	−0·061	+	0
Erythrocyte sodium concn.	−0·104	−0·317*	−0·173	−	0
Catalase activity	0·197	−0·007	−0·098	+	0
Mean corpuscular fragility and:					
Erythrocyte potassium concn.	−0·045	0·038	0·043	+	+
Erythrocyte sodium concn.	−0·053	0·015	−0·008	−	−
Catalase activity	−0·121	−0·117	0·101	+	∓
Erythrocyte potassium concn. and:					
Erythrocyte sodium concn.	0·237	−0·224	0·312**	−	−
Catalase activity	−0·234	0·174	0·060	+	∓
Erythrocyte sodium concn. and:					
Catalase activity	−0·256	−0·521**	−0·051	−	±

* $P < 0·05$. ** $P < 0·01$.

† Mean of February and August determinations, with exception indicated by following footnote.

‡ Correlations shown are between August values of mean corpuscular volume and mean corpuscular haemoglobin concentration. Correlations between August and February values of these characters, respectively, were −0·110, 0·019, and −0·020.

§ Symbols indicate whether the two characters differ between groups in the same (+) or opposite (−) direction, or show variable (∓, ±) or no (0) association.

cell volume. It does not represent a relationship between stable differences between animals (see footnote, Table 7).

Red cell sodium concentration [Na_e^+] shows several significant correlations, most notably with red cell count. [Na_e^+] is calculated from packed cell volume and the concentrations of sodium in whole blood and plasma. Derivation of [Na_e^+], unlike that of [K_e^+], involves estimation of a small difference between the two large values for blood and plasma sodium. Any error in this difference or in packed cell volume would lead to a positive correlation between [Na_e^+] and packed cell volume. Although values of [Na_e^+] must be regarded as imprecise, the correlations between [Na_e^+] and red cell count appear too high to be ascribed to error. [Na_e^+] determined in February is as strongly correlated with haemoglobin, packed cell volume, and count determined in August as it is with the February packed cell volume which enters into its calculation. The tendency for high [Na_e^+] to be associated with small cell size is consistent with its association with high cell count. The tendency to negative correlation between [Na_e^+] and catalase is of uncertain significance and meaning.

The relationship between [Na_e^+] and [K_e^+] is not consistent. The positive correlation in F_1 calves (Table 7) is balanced by the following results on cows:

British dams of British calves: $r = -0 \cdot 386$ (d.f. $= 24$, $P = 0 \cdot 05$).
British dams of F_1 calves: $r = -0 \cdot 280$ (d.f. $= 78$, $P < 0 \cdot 05$).
F_1 dams of F_2 calves: $r = 0 \cdot 152$ (d.f. $= 48$).

(e) *Relationships between Red Cell Characters and other Characters*

In Table 8 are listed correlations between red cell characters and the following other characters of the calves: body weight gain during summer, body weight at 2 years of age, mean coat score as yearlings, and protein-bound iodine determination of February. High coat scores signify long woolly coats, and are associated with relative unthriftiness (Turner and Schleger 1960; Turner 1962). The correlations are again calculated within breed group, sex, and haemoglobin type. Red cell count is again taken as representative also of results for packed cell volume and haemoglobin.

The F_1 calves showed no significant correlations, with the exception of that between coat score and body weight. This is typical of these first-cross animals which are rather uniform and appear insensitive, in growth rate, to physiological variables. In the other groups there was a moderate correlation between red cell count and growth and coat score. Other details of results not shown suggest that correlations with growth were lower for packed cell volume and slightly lower for haemoglobin than for red cell count. Also, packed cell volume and haemoglobin determined in summer and in winter were more closely related to contemporaneous gain than to gain in the other season.

The one significant correlation between mean corpuscular volume and body weight may merely reflect the relationship of that character to red cell count.

The slight evidence that high cell fragility is associated with high coat score and is therefore unfavourable receives some support from the correlation between median corpuscular fragility of dams and two-year-old weight of their calves: $r = -0 \cdot 459$ (British, $P < 0 \cdot 05$), $-0 \cdot 226$ (F_2, n.s.), $-0 \cdot 222$ (F_1, $P < 0 \cdot 05$).

TABLE 8

RELATIONSHIPS BETWEEN RED CELL CHARACTERS AND OTHER ANIMAL CHARACTERS, AS BETWEEN ANIMALS OF SAME BREED, SEX, AND HAEMOGLOBIN TYPE

Character	Summer Gain			Body Weight (2 years old)			Coat Score			Protein-bound Iodine		
	British	F_2	F_1	British	F_2	F_1	British	F_2	F_1	British	F_2	F_1
Degrees of freedom	25	48	95	25	48	95	25	48	95	25	48	95
Red cell count	0·424*	0·275	0·097	0·375	0·322*	−0·102	−0·385*	−0·117	−0·017	0·223	0·178	0·074
Mean corpuscular haemoglobin concn.†	0·199	0·128	0·099	0·314	0·048	0·020	−0·160	−0·225	−0·087	0·074	−0·194	−0·177
Mean corpuscular volume	−0·234	−0·213	−0·179	−0·416*	−0·084	0·187	0·211	−0·042	−0·170	0·045	−0·060	0·173
Mean corpuscular fragility†	0·009	0·158	0·108	−0·083	−0·036	−0·099	0·187	0·321*	−0·050	0·038	−0·112	0·006
Erythrocyte potassium concn.	−0·018	−0·046	0·082	0·021	−0·285*	−0·100	0·064	0·433**	0·019	0·215	−0·294	0·091
Erythrocyte sodium concn.	0·458*	−0·293*	−0·021	0·192	−0·050	−0·030	0·037	−0·198	−0·057	0·167	−0·143	0·042
Catalase activity†	0·149	0·198	0·063	0·112	0·000	−0·063	−0·136	−0·039	−0·025	0·082	0·135	−0·064
Summer gain				0·416*	0·376**	0·085	−0·419**	0·025	−0·088	0·305	0·474**	−0·079
Body weight							−0·636**	−0·248	−0·433**	0·102	0·336*	−0·116
Coat score										−0·186	−0·304*	−0·079

* $P < 0·05$. ** $P < 0·01$. † Mean of February and August determinations.

In the F_2 calves high red cell potassium concentration was associated with low body weight and protein-bound iodine and high coat score.

None of the red cell characters showed any evidence of relationship to the elevation of rectal temperature suffered by the calves under warm conditions. Nor were there any relationships to β-globulin (transferrin) types.

IV. Discussion

The picture of breed differences in red cell characters, presented by Evans (1963), is supplemented in some characters and details by these data. In packed cell volume, haemoglobin levels, red cell count, and red cell potassium concentration there were significant stepwise differences from Grade Brahman, through Brahman cross and Africander cross, to British calves. In median corpuscular fragility and catalase activity, on the other hand, Africander cross and British calves seemed indistinguishable, but were both markedly different from calves with Brahman breeding.

Breed differences in red cell characters are not accounted for at all by the presence of the gene for fast-moving haemoglobin in Zebu-type animals. On the contrary, the small proportion of Zebu animals that carry this gene are more like British animals in red cell characters than are those that lack it. Packed cell volume, haemoglobin level, and red cell count are lower, and fragility and potassium concentration are higher, in type AB than in type AA, and in British than in Zebu. None of the deviations associated with type AB haemoglobin appear advantageous, nor are its relationships with growth rate clear at this stage. Crockett, Koger, and Chapman (1963) found no effect of haemoglobin type of cows in Florida on growth rate of their calves, and we have found an indication of opposite effects in different progeny groups. Type B haemoglobin may have selection advantage, responsible for its maintenance in some breeds, only in particular genetic or environmental settings.

The haemoglobin types of sheep and cattle, allowing for their opposite nomenclature, are closely analogous both in the red cell characters with which they are associated and in some aspects of the pattern of geographic distribution, the slow-moving haemoglobin (bovine A, ovine B) tending to predominate in temperate–intensive conditions.

The evidence of segregation of catalase activity suggests that a large part, though probably not all, of genetic variation in catalase activity is controlled at a single locus, and that this locus is linked with the haemoglobin locus. Allison, Rees, and Burn (1957) postulated a single pair of alleles controlling catalase activity in dog erythrocytes, with the heterozygote intermediate in activity, and quoted a report by Putilin (1929) of a similar phenomenon in cattle.

Miller (1958), in a study of a variety of human patients, concluded that catalase activity of blood bears a constant relationship to haemoglobin concentration, and suggested that this constancy reflects a common metabolic pathway for the formation of haemoglobin and catalase. This observation is not true of cattle, in which marked differences occur in catalase activity per unit of haemoglobin. If some kind of association between catalase and haemoglobin type is to be found, a direct association might be expected, based on their chemical similarity. It is surprising therefore that the evidence available suggests linkage rather than pleiotropism. A direct association between haemoglobin type and catalase activity, consistent with the available evidence, could exist if the haemoglobins recognized as electrophoretically slow- and fast-moving were each divisible into subtypes such that A_1 and B_1 were associated with low catalase activity and A_2 and B_2 with high activity.

Catalase activity is expressed quantitatively in terms of its action on hydrogen peroxide. Differences in level of activity do not, of course, necessarily imply differences in quantity of catalase, but could be related to binding of the enzyme to stroma or, more probably, reflect qualitative differences in molecular type.

It is believed (Bingold 1935; Lemberg and Legge 1949) that a function of erythrocyte catalase is to protect haemoglobin against oxidative degradation and the cell against the fragility and aging consequent on this degradation (Ponder 1951). In data presented here, differences in catalase activity showed no consistent relationship with characters which might reflect differences in aging or life span, such as red cell count, fragility, or potassium concentration.

The fact that estimation of $[Na_e^+]$ is subject to considerable error has been pointed out. It is believed that this is responsible for the lack of evidence of its heritability. The conservative conclusion is that $[Na_e^+]$ and $[K_e^+]$ vary inversely, but the greater reliability of $[K_e^+]$ estimation makes it the better index of electrolyte balance. Nevertheless, the evidence (Table 7) that $[Na_e^+]$ shows correlations with other characters not shown by $[K_e^+]$ warrants further investigation.

In comparing individual animals, little association has been found between erythrocyte characters and animal performance. Red cell count (or packed cell volume or haemoglobin) is the most consistently related to growth rate. It has been suggested (Findlay 1950; Walker 1958) that haemoglobin level is specifically relevant to tropical adaptation. Although moderately heritable, it is known to be labile under nutritional and other environmental influences and its moderate correlation with growth rate probably arises from its acting as an index of general physiological status. There is some indication that high red cell potassium concentration and fragility are unfavourable characters but information at present available does not suggest that they would be useful characters in selection.

A picture has been presented (Evans 1963 and herein) of breed differences in red cell count, fragility, potassium concentration, catalase activity, and haemoglobin types. On this basis, the first four of these characters, at least, might have represented different aspects of one underlying phenomenon. It now appears, from data quite adequate to demonstrate high repeatabilities and heritabilities of these characters within breeds, that they are not correlated with each other. The red cell therefore presents a constellation of rather striking genetic differences, and a challenge to find functional reasons for their maintenance. It may be that differences in these characters are significant only in rather complex interactions with each other and with other variable characters.

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