Transferrin and post-albumin polymorphism in East African cattle

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1. INTRODUCTION

Gene frequencies for the three transferrin alleles in European breeds of beef and dairy cattle are reasonably well established (Ashton, 1958; Schmid, 1962). Comparable frequencies for Zebu breeds have been reported so far only by Ashton (1959) and then only from small numbers of Zebu cattle imported into Australia, and their progeny from crosses with European cattle. This paper reports data for some East African breeds. Post-albumin phenotypes (Ashton, 1963) were also determined on the samples available, and gene frequencies for the polymorphism calculated for the breeds examined.

The cattle chosen for sampling were from herds which were considered likely to represent the breed as a whole. However, the gene frequencies presented here are herd gene frequencies and may be only an approximation to the true breed gene frequencies.

2. MATERIALS AND METHODS

Breeds sampled represented the main cattle types found in East Africa as listed by Mason (1951). Sanga cattle were represented by the Ankole breed, East African Shorthorned Zebus by the Tanganyika Shorthorned Zebu, Boran and Teso (Bukedi) breeds and Sanga × Shorthorned Zebu by the Nganda breed. In addition a herd of Sahiwal (Indian Zebu) cattle resident in Kenya was examined.

The 267 serum samples from Ankole cattle were collected from two farms belonging to the Uganda Department of Veterinary Services and Animal Industry at Mbarara and Ruhengere. Both these herds had been derived from a common source and throughout this paper the data resulting from the Ankole samples have been treated as if they were derived from one herd. The Teso and Nganda cattle also belonged to the Uganda Department. The seventy-two samples that were obtained from the former came from a foundation herd maintained at the Livestock Husbandry Experimental Unit, Nakyesasa, whilst the 138 samples from Nganda

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Table 1. Number of transferrin phenotypes observed in six populations of East African cattle, and number expected calculated from the gene frequencies in Table 2

| | | 228 53 228·0 | | | •• | • • | | • | | 12.0 | •• | •• |
|-----------|---------|--|--------|-------|-------|-------|------------|---------------------|------|-------|----------|-------|
| | | 8 10.53 | | | •• | •• | | | | 8.34 | | ••• |
| | म | 38 36-75 | 11 | 9.5(| 52 | 55.85 | 22 | 17.95 | | 15.99 | 4. | ۷. |
| | FF | $\frac{29}{32.06}$ | 0 | 3.83 | 36 | 35.04 | 17 | 17-37 | 7 | 7.67 | ∞ | 12.17 |
| | DE | 27 24·07 | 10 | 6.61 | 31 | 29.67 | 7 | 98.9 | 9 | 5.78 | 22 | 17.60 |
| | DF | 46 42·00 | 23 | 5.33 | 37 | 37.23 | 6 | 13.27 | 9 | 5.55 | 13 | 10.03 |
| ļ | DD | 12 13·75 | ಣ | 1.85 | 11 | 68.6 | ಣ | 2.53 | 0 | 1.00 | 1 | 2.07 |
| type | BE | $\begin{array}{c} 12 \\ 9.46 \end{array}$ | 9 | 5.16 | 11 | 10.76 | - | 1.61 | အ | 1.70 | 16 | 17.60 |
| Phenotype | BF | 17 16·50 | 4 | 4.17 | 18 | 13.50 | ō | 3.12 | 0 | 1.63 | 10 | 10.03 |
| | BD | 7 10·81 | 4 | 2.90 | က | 7.17 | 0 | 1.19 | 0 | 0.59 | က | 4.14 |
| | BB | $\begin{array}{c} 2 \\ 2.12 \end{array}$ | 0 | 1.13 | 1 | 1.30 | | 0.14 | 0 | 0.09 | က | 2.07 |
| | AE | 5 6.66 | 26 | 23.95 | 15 | 12.21 | 12 | 10.29 | 9 | 8.85 | 49 | 47.20 |
| | AF | $\begin{array}{c} 12 \\ 11.63 \end{array}$ | 29 | 19.34 | 13 | 15.32 | 19 | 19.91 | 11 | 8.49 | 30 | 26.91 |
| | AD | 8 7.62 | 10 | 13.44 | 0 | 8.14 | 12 | 7.60 | 5 | 3.07 | 7 | 11.09 |
| | AB | 4 2.99 | 11 | 10.50 | က | 2.95 | 0 | 1.79 | 23 | 0.90 | 12 | 11.09 |
| | , AA | $\frac{1}{1\cdot05}$ | 20 | 24.38 | 1 | 1.67 | 4 | 5.70 | _ | 2.35 | 14 | 14.87 |
| Obs. | | Obs. Exp. | | | | | Obs. | Exp. | Obs. | Exp. | | |
| | Breed | Sahiwal | Nganda | | Boran | | Tanganyika | Shorthorned Zebu | Teso | | Ankole | |

cattle came from the Animal Health Research Centre at Entebbe. The Boran herd from which 265 samples were obtained was the one kept at Muguga by the East African Veterinary Research Organization, the breeding of which has been described by Lampkin & Lampkin (1960). The 114 samples obtained from the Tanganyika Shorthorned Zebus came from the Tanganyika Government Livestock Research Centre at Mpwapwa, whilst the 228 Sahiwal samples were obtained from the National Sahiwal Stud maintained by the Kenya Department of Veterinary Services at Naivasha, a station situated about 50 miles west of Nairobi.

Starch gel electrophoresis

The serum samples were examined by starch gel electrophoresis in a discontinuous tris-citric, boric acid-lithium hydroxide system. Details of this procedure have been published (Ashton & Lampkin, 1965).

3. RESULTS

Transferrins

All fifteen phenotypes described by Ashton (1959) were found in the cattle sera examined, representing the homozygotes and heterozygotes of the alleles Tf^A , Tf^B , Tf^D , Tf^E and Tf^F . In addition a further phenotype Tf GF (Ashton & Lampkin, 1964) was found in three Borans. These animals have not been included in the analysis of the transferrin results because of the infrequency of this phenotype.

Table 1 shows the numbers of each transferrin phenotype observed in each of the breeds examined. Table 2 shows the gene frequencies derived from these

Table 2. Transferrin gene frequencies and standard errors for six populations of East African cattle, calculated from the observed phenotype distribution shown in Table 1

| \mathbf{Breed} | Tf^{A} | Tf^{B} | Tf^D | Tf^F | Tf^E |
|------------------|-------------|-------------|-------------|-------------|-------------|
| Sahiwal | 0.068 | 0.096 | 0.246 | 0.375 | 0.215 |
| | ± 0.012 | ± 0.014 | ± 0.020 | ± 0.023 | ±0.019 |
| Nganda | 0.420 | 0.091 | 0.116 | 0.167 | 0.206 |
| | ± 0.030 | ± 0.017 | ± 0.019 | ± 0.022 | ± 0.024 |
| Boran | 0.080 | 0.070 | 0.194 | 0.365 | 0.291 |
| | ± 0.012 | ± 0.011 | ± 0.017 | ± 0.021 | ± 0.020 |
| Tanganyika | 0.224 | 0.035 | 0.149 | 0.390 | 0.202 |
| Shorthorned Zebu | ± 0.030 | ± 0.011 | ± 0.023 | ± 0.032 | ± 0.023 |
| Teso | 0.181 | 0.035 | 0.118 | 0.326 | 0.340 |
| | ± 0.032 | ± 0·015 | ± 0.027 | ± 0.039 | ± 0.040 |
| Ankole | 0.236 | 0.088 | 0.088 | 0.214 | 0.374 |
| | ± 0.018 | ± 0.012 | ± 0.012 | ± 0·018 | ± 0.021 |

data, and their standard errors. Table 1 also shows the numbers of each phenotype expected, assuming genetic equilibrium, calculated from the derived gene frequencies.

Post-albumins

The three post-albumin phenotypes PaF, PaFS, and PaS found in European cattle (Ashton, 1963) were represented in each breed examined except Nganda. In this breed only PaF and PaFS types were found.

Table 3 shows the numbers of each post-albumin phenotype found in each of the breeds examined. The three Borans with transferrin type TfGF were included in Table 3, but one other Boran sample could not be typed on initial electrophoresis

Table 3. Number of post-albumin phenotypes observed in six populations of East African cattle, and number expected calculated from the gene frequencies in Table 4

| | Obs. | | | | |
|-----------------------------|------|----------------|------------------------|-------|--------|
| | or | | | | |
| Breed | exp. | ${f F}$ | $\mathbf{F}\mathbf{S}$ | S | Totals |
| Sahiwal | Obs. | 49 | 106 | 73 | 228 |
| | Exp. | 45.64 | 112.74 | 69.62 | 228.0 |
| Nganda | Obs. | 104 | 34 | 0 | 138 |
| | Exp. | 106.09 | 29.82 | 2.09 | 138.0 |
| Boran | Obs. | 121 | 123 | 21 | 265 |
| | Exp. | $125 \cdot 69$ | 113.63 | 25.68 | 265.0 |
| Tanganyika Shorthorned Zebu | Obs. | 82 | 29 | 3 | 114 |
| | Exp. | 81.69 | 29.62 | 2.69 | 114.0 |
| Teso | Obs. | 39 | 29 | 4 | 72 |
| | Exp. | 39.76 | $27 \cdot 49$ | 4.75 | 72.0 |
| Ankole | Obs. | 120 | 121 | 26 | 268 |
| | Exp. | $122 \cdot 01$ | 116.96 | 28.03 | 268.0 |

and the sample was lost before it could be repeated. Gene frequencies and their standard errors derived from Table 3 are shown in Table 4. Table 3 also shows the numbers of each phenotype expected, assuming genetic equilibrium, calculated from the gene frequencies.

Table 4. Post-albumin gene frequencies and standard errors for six populations of East African cattle, calculated from the observed phenotype distribution shown in Table 3

| \mathbf{Breed} | Pa^F | Pa^S |
|-----------------------------|-------------------|-------------------|
| Sahiwal | 0.447 ± 0.023 | 0.553 ± 0.023 |
| Nganda | 0.877 ± 0.020 | 0.123 ± 0.020 |
| Boran | 0.689 ± 0.020 | 0.311 ± 0.020 |
| Tanganyika Shorthorned Zebu | 0.847 ± 0.024 | 0.153 ± 0.024 |
| Teso | 0.743 ± 0.037 | 0.257 ± 0.037 |
| Ankole | 0.676 ± 0.020 | 0.324 ± 0.020 |

4. DISCUSSION

Table 2 shows that each of the five transferrin alleles previously found in Sindhi and Sahiwal dairy cattle (Ashton, 1959) were represented in each of the breeds examined. In addition a further allele, Tf^{G} , was found in three of the Borans (Ashton & Lampkin, 1965). These East African cattle differ markedly from European cattle in transferrin constitution, having three alleles Tf^{B} , Tf^{F} , and Tf^{G} not found in European breeds.

In all the East African breeds examined except Nganda, Tf^E and Tf^F together account for 59–66% of the transferrin alleles. In Nganda cattle Tf^A was most frequent, displacing Tf^E and Tf^F . This is an old-established herd and the use of

only a few sires could have accounted for this. In all the breeds, however, Tf^B was very infrequent (less than 10%). The reasons for the predominance of Tf^E and Tf^F types are not known. In nearly all European breeds examined Tf^E is the least frequent allele (see, for example, Schmid, 1962), and in some breeds (Jersey, Guernsey) Tf^E may be absent in some locations.

The frequencies for the two post-albumin alleles (Table 4) were similar for all breeds except Sahiwal. Pa^F is two to three times more frequent than Pa^S , except in Sahiwals where Pa^S is slightly more frequent than Pa^F . These frequencies differ markedly from European breeds where Pa^S is the predominant allele, and the frequency of Pa^F is low or zero (Ashton, unpublished observations).

Both polymorphic systems examined in these East African cattle show marked differences from European breeds. It is speculative whether Tf^B , Tf^F , Tf^E , and Pa^F are more frequent in Zebu cattle because they have special advantage for these animals in their native environment, or whether the gene frequency difference is merely a reflexion of the genotype of the ancestors of the two types of cattle.

Maintenance of a stable polymorphism is commonly brought about by superior fitness of the heterozygotes, resulting in a relative excess of heterozygotes in the population. Evidence suggesting superior fitness of the common heterozygote in European dairy cattle comes from the time distribution of returns-to-service following insemination. Ashton & Fallon (1962) found that matings between TfAA and TfDD parents, producing only TfAD offspring, gave 21.8% of the service returns 25 days or later following insemination. The mean figure for all other matings was about 31%. A similar effect has been observed by the New Zealand Dairy Production and Marketing Board (1963). TfAA × TfDD matings gave 16% of service returns in the period 25–49 days after insemination, while the mean figure for all other matings was about 27%. Assuming that long returns (i.e. post 25 days) bear a relationship to embryonic loss this implies that heterozygotes are more viable in utero. A relative excess of heterozygotes would be expected in a dairy cattle population as a result.

The data in Table 5 show that 4.2% more transferrin heterozygotes were found than expected by calculation. An excess of heterozygotes is normally obtained by this method of calculation and amounts to 1/8 S, where S is the number of sires in use in the herds sampled (Robertson, 1965). The number of effective sires in these East African herds is not known, but will have been the same for both transferrin and post-albumin systems. The excess of heterozygotes at the post-albumin locus was 2.7%. If it is assumed that this is due solely to the limited use of sires and to the method of calculation then this is the approximate extent of the excess expected at the transferrin locus. The difference of 1.5% between the two heterozygote excesses is not significant, but suggests that a true excess of heterozygotes may have been present in these East African cattle. Further surveys in which concurrent analyses of transferrin and other serum polymorphisms are made may throw light on the difficult problem of determining whether or not a transferrin heterozygote excess exists in cattle populations. A survey in 293 Droughtmaster cattle in Queensland (Ashton, Francis & Ritson, unpublished data) gave a

transferrin heterozygote excess of 7.03% and a post-albumin heterozygote excess of 2.54%.

The extent of the transferrin heterozygote excess may be quite small, and yet sufficient to maintain a stable polymorphism. It is known that heterozygote fitness superiority of the order of 1% is sufficient (Blumberg, 1961). In a two-allele system

Table 5. Homozygotes and heterozygotes observed and expected for transferrin and post-albumin polymorphism in six populations of East African cattle

| | | Trans | ferrins | | Post-albumins | | | | |
|------------------------|--------------|------------------|---------|-----------------------|---------------|----------------|--------|----------------|--|
| Breed | Homo Obs. | ezygotes Exp. | Hetero | Exp. | Homo Obs. | Exp. | Hetero | exp. | |
| Sahiwal | 52 | 59.51 | 176 | 168-49 | 122 | $115 \cdot 26$ | 106 | 112.74 | |
| Nganda | 25 | 37.07 | 113 | 100.93 | 104 | 108-18 | 34 | 29.82 | |
| Boran | 71 | 70.16 | 192 | $192 \cdot 84$ | 142 | $151 \cdot 37$ | 123 | 113.63 | |
| Tanganyika Shorthorned | | | | | | | | | |
| Zebu | 27 | 30.38 | 87 | 83.62 | 85 | 84.38 | 29 | 29.62 | |
| Teso | 17 | 19.45 | 55 | $\bf 52 \!\cdot\! 55$ | 43 | 44.51 | 29 | $27 \cdot 49$ | |
| Ankole | 60 | 68.63 | 207 | 198.37 | 146 | 150.04 | 121 | 116.96 | |
| Totals | 252 | $285 \cdot 20$ | 830 | 796 ·80 | 642 | 653.74 | 442 | $430 \cdot 26$ | |

a loss of 5% of homozygotes from all matings in which equal numbers of homozygotes and heterozygotes would be expected will lead to a true heterozygote excess of 1.9% in the population by the usual method of calculation.

SUMMARY

The serum transferrin and post-albumin phenotype distributions of 228 Sahiwal, 138 Nganda, 265 Boran, 114 Tanganyika Shorthorned Zebu, 72 Teso and 267 Ankole cattle from East Africa were determined.

Five transferrin alleles, Tf^A , Tf^B , Tf^D , Tf^E , and Tf^F were present in all the breeds examined, and a sixth allele, Tf^G , was present in three of the Borans. Tf^E and Tf^F were the most frequent alleles, except in the Nganda cattle where Tf^A was the most frequent. Tf^B had a frequency of less than $0\cdot 1$ in each breed. Two post-albumin alleles, Pa^F and Pa^S , were present in each breed. In each breed except Sahiwal Pa^F was two to three times more frequent than Pa^S . In the Sahiwal Pa^F and Pa^S had about the same frequency. It was concluded that both transferrin and post-albumin gene frequencies in East African cattle differ significantly from the corresponding frequencies in European cattle.

There was no evidence of an excess of heterozygotes in the post-albumin system other than that expected from the use of relatively small numbers of bulls in these herds. However, allowing for the same factor in the transferrin system, there appeared to be an excess of transferrin heterozygotes in the cattle populations sampled although the extent of this excess could not be calculated accurately.

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