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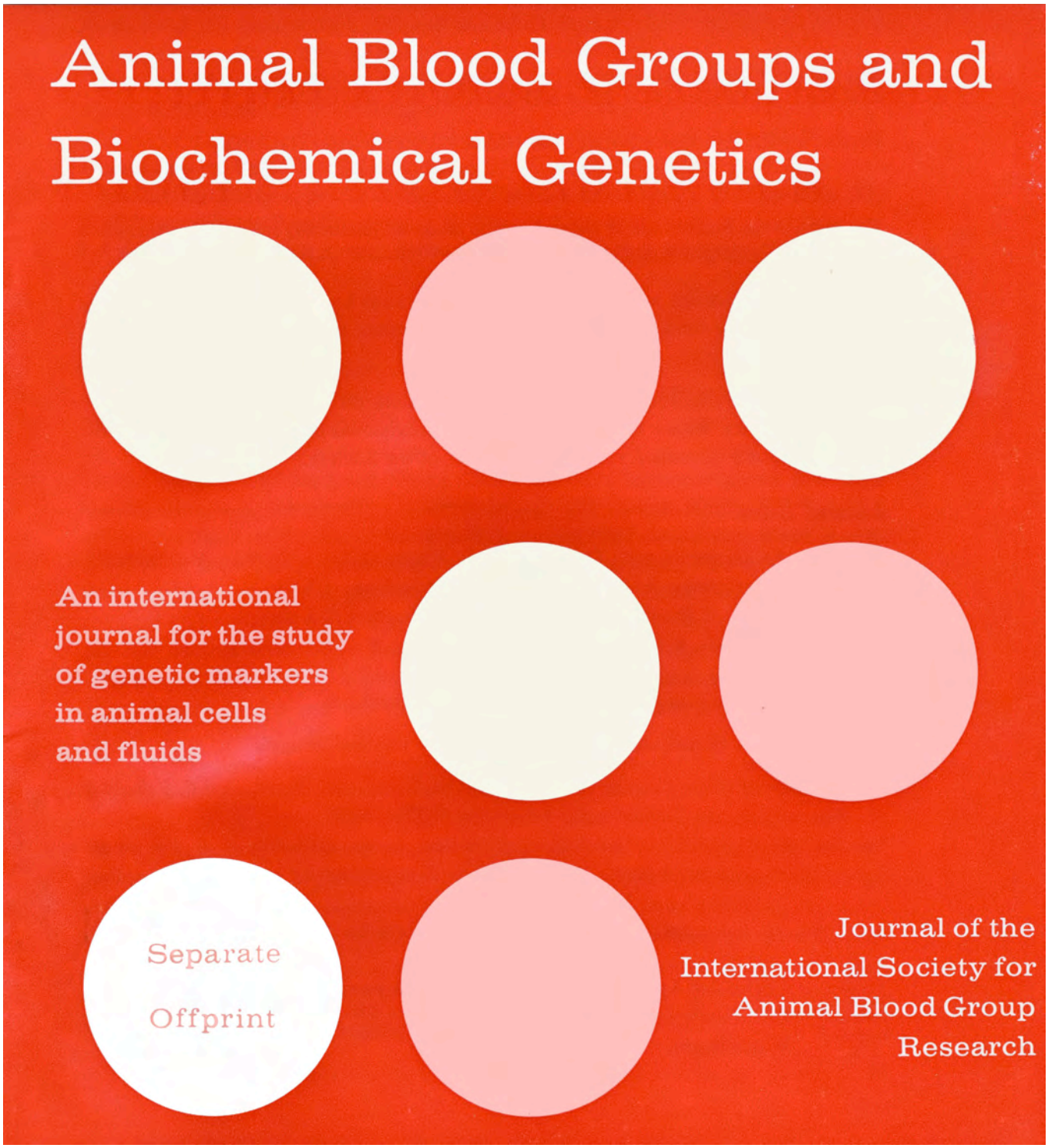

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The use of genetic relationships among cattle breeds in the formulation of rational breeding policies: an example with South Devon (South Africa) and Gelbvieh (Germany)*

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Summary

At the instigation of the South Devon Cattle Breeders' Society of South Africa we studied the genetic relationships of South Devon cattle (South Africa) and Gelbvieh cattle (Germany) with eight other breeds including Red Angus and Black Angus (USA). On the basis of comparisons at ten immungenetic loci Gelbvieh and South Devon cattle are nearly as genetically similar as Red and Black Angus. The results indicate that Gelbvieh and South Devon had a common ancestry on the Continent and are distinct from other British breeds such as Hereford, Angus and Jersey. This study illustrates the application of studies of the genetic similarities of different breeds to the rational development of future breeding and preservation programs.

Introduction

When a reproductive barrier arises between two parts of a population, the two isolated populations begin to diverge. For domestic animals this barrier may be artificial, or it may be geographical as in many natural populations. In any case, divergence results for one or more of a variety of reasons: random genetic drift, natural selection and adaptation to different environments, and artificial selection.

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There is no accurate way to judge when such divergence has become sufficiently large to designate the two populations as separate breeds, because the definition of a breed is not at all consistent and may vary greatly from population to population. In some cases a group of animals imported into a country may be called a new breed immediately. In others, a difference in a single genetic locus controlling coat color may provide the basis for two separate breeds, for example the Red and Black Angus breeds in the USA and the Schwarzbuntes and Rotbuntes Niederungsvieh breeds of the Low Countries. In contrast, there may be several color and pattern loci segregating within a single breed as in Icelandic cattle. In some countries, such as Norway, the recent policy has been to fuse breeds that were closely related on the basis of common distinguishing characteristics, even though there were some observable differences between them. Thus, the decisions concerning the degree of dissimilarity at which two populations are called different breeds and the degree of similarity at which two closely related breeds are melded into one are variable and arbitrary. However, studies of the relative genetic similarities of breeds can provide a useful objective basis for such decisions.

The present study was undertaken at the instigation of the South Devon Cattle Breeders' Society in South Africa. The Society wishes to improve the South Devon cattle through an infusion of genes from outside South Africa, specifically of genes from the Gelbvieh cattle of Germany. Unfortunately, the rules of the Stud Book Association prevent registration of animals from crosses with cattle of different breeds. However, if Gelbvieh and South Devon were genetically very closely related, then such crossing might be acceptable to the Stud Book Association. Since some cattle breeders thought these two breeds might be closely related, we were asked to do an analysis of their genetic similarity.

The two breeds

The South Devon breed was developed in Devon and Cornwall in southwestern England. The time of introduction to this area and the origin of the parent stock are unknown (French et al., 1966). The cattle are thought to have originated on the Channel Isles, descended from animals believed to have come from Normandy and Brittany. The South Devon was first introduced to South Africa in Natal, probably in the 1890's as pedigree animals of the breed became known at the Natal Royal Shows in Pietermaritzburg, soon after this time (Osterhoff, unpublished).

South Devon cattle are found throughout the world: Australia, New Zealand, Brazil, China, Japan, Spain, Chile, Cyprus, USA, Canada, Ireland, Mexico, West Indies and, as mentioned above, in England and South Africa. However, the breed is less popular today than in the past, probably for several reasons: the animals often have too coarse a conformation, have narrow thurl bones and pin bones with a narrow high tail setting, and have shoulders that arc loose, coarse or very

forward. The South Devon cattle in South Africa are heavy of bone and thus give a relatively low slaughtering weight, although the quality of meat is fairly good; they are somewhat slow maturing and weak in overall muscling, especially in round of beef. The South Devon breeders felt that improvement, especially in the last-mentioned traits, could be obtained relatively easily by using Gelbvieh semen on the South Devon cows.

The origin of Gelbvieh goes back to the red to red brown celtic-german landrace. Beginning in 1810 large farms took over the initiative in crossbreeding this landrace with other breeds. Among these the Heilbronn Landrace, the Simmental and the Shorthorns had the most lasting influence (French et al., 1966). After many setbacks, pure breeding was started about 1920 on pilot breeding stations. The cattle were selected for uniform color, draught capacity, and growth. Soon the fattening performance, the carcass quality, and the tenderness of the beef became well known. Gelbvieh cattle are well muscled, have good size and length, and grow fast. The breed also has an enviable reputation for its milk production. German Gelbvieh are bred primarily in Franconia, a region of Bavaria; the total population is about half a million.

As summarized above, the histories of these two breeds provide no evidence that they might be closely related. However, the ultimate origins of the breeds are sufficiently vague that the possibility of a close relationship cannot be excluded. Previous genetic studies offer little additional information; the two have never been directly compared. Bangham (1957) showed that South Devon and the Channel Island breeds have hemoglobin B and thereby differ from other British breeds. Osterhoff (1968) confirmed the difference from other British breeds in his comparison of 18 different breeds either imported or indigenous to South Africa. A study of Southern German breeds (Erhard & Schmid, 1964, 1965) did not clarify the origins of Geibvieh. Kidd & Pirchner (1971) showed that the Austrian yellow cattle, which are historically related and genetically similar to the Gelbvich in Germany, are not closely related to any of the other nine breeds they studied. Thus, the genetic data available do suggest that neither breed is closely related to any other breed with which it has been compared.

Measurement of breed relationships

It is a striking fact that both the Gelbvieh and the South Devon show uniform yellow brownish color. Such phenotypic traits as color, pattern, horn type, etc. are due to only a small number of loci and can be rather rapidly modified by artificial selection. Therefore, they are not ideal measures of overall genetic similarity. The best estimate of breed relationships is genetic similarity using cryptic polymorphisms (blood groups, enzymes and serum proteins) because these genes will be less responsive to artificial selection and will give a more unbiased estimate of overall genetic similarity. Obviously, as with any statistical estimate, the more loci used, the greater the accuracy.

Cavalli-Sforza (1969) proposed a modified f statistic based on the angular transformation that could be used for di-allelic and multi allelic loci to calculate an average value estimating the Wahlund's variance between two populations (see also Kidd & Cavalli-Sforza, 1974):

$$f_\theta = 4\sum_i (1 - \cos\Theta_i) \Big/ \sum_i (k_i - 1)$$

where summation is over all loci, k, is the number of alleles for the *i*th locus, and $\cos\Theta_i$ is calculated for the *i*th locus with:

$$\cos\Theta_i = \sum_{j=1}^{k_i} \sqrt{p_j p'_j}$$

where summation is over all alleles at that locus and p_j and p'_j, are the frequencies of the jth allele in the two populations being compared. This f_θ vaiue is a distance measure between two populations: the smaller the value the greater the genetic similarity, the larger the value the less the genetic similarity. Whereas this value can be related theoretically to random genetic drift and to divergence under selection, it is sufficient in itself for our present purpose. We are concerned here not with the mechanisms that have led to genetic divergence, but only with its magnitude.

Blood group, hemoglobin, and transferrin phenotypes were collected for our studies. Gene frequencies for the South Devon cattle in South Africa were based on 348 animals typed by Osterhoff (1968) and 200 animals typed by Erhard (unpublished). All samples were used to calculate gene frequencies for all systems except the B system which was based only on the 200 samples typed by Erhard. The gene frequencies for the Gelbvieh were based on 244 samples typed by Erhard (unpublished). Data on the remaining breeds were collected from herds in the USA by Stone and Kidd (unpublished). These latter breeds represent a variety of European origins and were included for comparison. Allele frequencies for the following ten loci (with number of alleles considered at each) were used to compare the ten breeds: the blood group loci *A*(3), *B*(4), *C*(3), *FV*(2), *J*(2), *L*(2), *M*(2) and *Z*(2), the hemoglobulin locus (2), and the transferrin locus (3). The exact allele frequencies used are available from the authors.

The *A*, *B* and *C* blood group systems require special treatment for these studies (Kidd & Pirchner, 1971; Kidd & Cavalli-Sforza, 1.974). The mathematical transformations are only statistically valid for allele frequencies between 0.05 and 0.95. While an occasional very rare allele introduces little error into the comparisons, large numbers of alleles with low frequencies reduce the accuracy of the comparisons to a large, but unmeasurable, extent and are thus not acceptable. This presents a particular problem with the very complex B system. Recombination within these systems is a further complication because it results in the formation of new rare alleles at a rate much higher than mutation and causes changes in allele frequencies more rapidly than drift. Because of these

complications, there is no completely satisfactory way to quantitatively compare phenogroup frequencies for these systems, though they can be informative in a non quantitative way (e.g. Braend et al., 1962). Since our objective is a quantitative study incorporating information from several independent loci, we have chosen to simplify the A, B, and C systems by reducing them to three (A_1, A_2, a), four (b, B, G, BGK), and three (C_1, C_2, c) 'alleles', respectively. These 'alleles' were obtained by considering only antigens A_1 and A_2; B, G, and K; C_1 and C_2. All phenogroups which were identical with respect to these antigens were treated as a single allele. This treatment allows us to incorporate into our calculations some information from these factor union systems (Cotterman, 1968); they would otherwise have to be omitted from the analysis. There should be no bias introduced since all breeds were treated identically.

Results

The matrix of pairwise f_θ values and their standard errors is given in Table 1. The standard errors were calculated with the ten separate values for the ten loci as independent estimates of f; the f_θ value presented is the weighted mean (Kidd & Cavalli-Sforza, 1974).

Certain biases affect these values. No correction has been introduced for the effect of the sample size upon which the gene frequencies were based. The calculated f_θ value should be reduced by approximately 1/N where N is the average of the

Table 1. The f_θ distance matrix with standard errors. The f_θ values for all pairs of breeds studied are given in the lower triangular matrix. The corresponding standard errors are given in the upper triangular matrix. Thus, the f_θ for Holstein (1) and Hereford (5) is the 1st column, 5th row and the standard error is in the 5th column, lst row: 0.176 ± 0.047.

		1	2	3	4	5	6	7	8	9	10
Holstein	1		0.071	0.028	0.023	0.047	0.042	0.024	0.042	0.023	0.024
Jersey	2	0.155		0.023	0.046	0.063	0.081	0.027	0.077	0.020	0.037
Brown Swiss	3	0.108	0.139		0.040	0.082	0.024	0.035	0.045	0.019	0.025
Guernsey	4	0.077	0.138	0.138		0.025	0.06	0.027	0.056	0.020	0.027
Hereford	5	0.176	0.252	0.216	0.135		0.067	0.028	0.069	0.056	0.062
Black Angus	6	0.087	0.212	0.131	0.160	0.206		0.046	0.018	0.052	0.035
Charolais	7	0.094	0.093	0.118	0.074	0.189	0.122		0.039	0.018	0.025
Red Angus	8	0.103	0.236	0.128	0.154	0.178	0.039	0.120		0.041	0.038
Gelbvieh	9	0.072	0.085	0.082	0.079	0.205	0.122	0.076	0.148		0.016
South Devon	10	0.080	0.152	0.081	0.097	0.146	0.096	0.093	0.134	0.045	

sample sizes of the two breeds being compared. Since all samples in this study were greater than 200, this factor has been ignored. The randomness of the sample is possibly more important. Were one sample to consist of a high proportion of closely related animals, the calculated f_θ values between that breed and the others would be increased. This may be an important factor in the Red Angus breed since many related animals were unavoidably included in our sample. However, the sample was large enough that this cannot have elevated the f_θ values by much and is probably negligible. Errors due to differences in blood typing reagents and errors in determining hemoglobin and transferrin types by gel electrophoresis are probably negligible as well since all three laboratories have regularly participated in the International Comparison Tests with a very high degree of concordance.

The most notable result is that the two smallest values are those for Red Angus – Black Angus ($f_\theta = 0.039 \pm 0.018$ and for South Devon – Gelbvieh ($f_\theta = 0.045 \pm 0.016$). These two f_θ values are not significantly different from each other and are considerably smaller than any other values in Table 1.

Discussion

Because different loci and/or measures of genetic distance have been used in other studies of cattle breed relationships, no direct comparison of these results with those of other studies is possible. However, some earlier results with the f_θ measure do allow general statements that are useful in evaluating the present results. The smallest values known between different breeds are among the Norse breeds (Kidd & Cavalli-Sforza, 1974) where f_θ is about 0.035. The smallest value of f_θ, yet found, 0.022, was between two separate samples of the cattle on Iceland (Kidd, unpublished). Thus, the values for the two most closely related pairs in this study (0.039 and 0.045) are of the same order as those for the Norse breeds and only slightly larger than. values for one pair of independent samples of Icelandic cattle.

Two possible biases were mentioned earlier: small sample size and related animals in a sample. Applying the correction for sample size reduces the GelbviehSouth Devon f_θ value to 0.042. The maximum effect of related animals in the Red Angus sample can be estimated by comparing the f_θ values involving Red Angus with those involving Black Angus. With the eight other breeds studied, Red Angus had an f_θ that was, on average, 0.009 greater than that of Black Angus. This excess is due to statistical error, a possible greater divergence in the Red Angus breed, and the inclusion of related animals in the sample, three factors that cannot be individually evaluated. Assuming, at worst, that it were all due to our sample, the Red Angus Black Angus f_θ would be reduced to 0.030. This value is not significantly different from the uncorrected f_θ for Gelbvieh and South Devon. Thus, the two smallest values from Table 1 are not significantly different as originally calculated nor after correction for possible biases.

Breeds with a very recent common ancestry should have some of the phenogroups at the B system in common. For reasons previously cited we cannot quantitatively evaluate the data on individual phenogroups. Moreover, because of the high sampling errors for the individual phenogroups, particularly in the South Devon sample, we have not even attempted a non quantitative comparison. We note only that 10 phenogroups out of approximately 40 in each breed are common to both Gelbvieh and South Devon. This value neither supports nor argues against our conclusions based on the simultaneous evaluation of data for all ten loci.

Clearly, relative to other breeds in this study and to other studies of breed relationships Gelbvieh and South Devon cattle are closely related breeds. However, it is a semantic question as to whether or not they are the same breed. On a purely legalistic basis they are not because they have been designated by man as different breeds. However, they are very similar genetically, at least with respect to ten immunogenetic loci that should reflect their relationship notwithstanding artificial selection. This similarity is of the same order as between Red and Black Angus, two breeds originally separated in the late 19th century but only slightly diverged because of continued gene flow, and as among some Norse breeds, possibly separated as much as 1000 years but showing little divergence. The differences between Gelbvich and South Devon are of the magnitude expected if they had a common origin and were separated from each other for only a few hundred years. Moreover, the relationships of these two breeds with the other eight breeds in our study suggest a common Continental origin that is distinct from that of Hereford, Angus and Jersey.

These conclusions are subject to two caveats: first, large standard errors were observed because few loci were used; second, the conclusions are limited to only the ten breeds in our study. It seems unlikely, though possible, that our conclusions would be substantially altered by the addition of data on more loci. Also, comparisons with the results of Kidd & Cavalli-Sforza (1974) and Kidd & Pirchner (1971) suggest that the conclusions can be extended to cover relationships to other breeds as well.

This study is a good illustration of the potential use of genetic data on domestic animal populations. Identification of the relationships of populations can greatly assist in the rational development of future breeding and preservation programs that will make optimum use of the germ plasm resources of the species. Mason (1972) has discussed the need for genetic studies of breeds before decisions on importation, cross breeding, upgrading, etc. are made. We feel these analyses justify the incorporation of Gelbvieh genes into the South Devon breed of South Africa in two ways. First, the herdbook rules would not be violated because it appears that the two breeds have a relatively recent common origin and have diverged genetically only about the amount expected from the separation of the two populations. Second, because of this similarity of the two breeds, the variation within the South Devon breed would be only moderately (but probably

sufficiently) increased without the singular qualities of the breed being completely destroyed.

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