Reprinted from EVOLUTION, Vol. 28, No. 3, October 22, 1974
pp. 38l–395
Made in United States of America

THE ROLE OF GENETIC DRIFT IN THE DIFFERENTIATION OF ICELANDIC AND NORWEGIAN CATTLE[1]

K. K. KIDD[2] AND L. L. CAVALLI-SFORZA
Department of Genetics, Stanford University Medical Center, Stanford, California 94305

Received April 20, 1973

Gene frequency differences between populations can arise from (1) random genetic drift, the accumulation of sampling variance over several generations, (2) selective forces acting differentially on the populations, (3) differential migration from a population with different gene frequencies, and/or (4) distinct mutation histories, resulting in the chance occurrence of a particular allele in one population, but not in others in the absence of migration equalizing such effect. If differential gene flow from outside has not occurred and no unique mutations are present, the problem of deciding between drift and selection as the cause of observed differences still remains difficult. The effects of selective forces can be predicted only if the selection coefficients are known, an exceedingly rare circumstance, but the expected magnitude of difference due to random genetic drift can be predicted on the basis of demographic data which are relatively easy to obtain. However, little is known about the historical demography of most species, man being the major exception. Another species for which both genetic and demographic data are available is domestic cattle.

The genetic data on cattle comes mostly from blood typing. Cattle blood typing has a long history (Stormont, 1962), and is routinely done in many countries as the best method of parentage control. The specific demographic ("bosographic") data we have analyzed come from Iceland and Norway. Comparable genetic data are also available on these breeds, providing a uniquely suitable material for comparing the expected genetic change due to drift with observed gene frequency differences: (1) they have been separated from each other, and probably all other breeds as well, for about 1000 years, a sizable length of time; (2) they are very likely to share a common origin in Norway; (3) there are some historical demographic data available on both Icelandic and Norwegian breeds, and (4) there are good genetic data available on the present day populations. With this material we shall study whether random genetic drift alone can account for the observed differences among Norse cattle breeds.

HISTORY

Iceland was colonized, starting over 1000 years ago, by Vikings (Thorsteinsson, 1946); the colonization lasted for about a century, after which there was little further movement onto the island. The actual proportion of Norsemen in the colonizing population is unknown. The tradition holds that colonists were mostly Norsemen, although they had some Celtic retainers (Irish). Early blood typing work on the present Icelandic population showed a close similarity with Ireland, Scotland, and Wales those parts of the British Isles of Celtic tradition(see a discussion in Mourant, 1954). More recent work suggests a Celtic origin for some markers and a Scandinavian one for others. Averaging indicates that a proportion of approximately two thirds Scandinavian to one third Celtic is the admixture (J. Edwards, A. E. Mourant, et al., pers. comm.).

[1]This research was supported in part by grants from the U.S.A.E.C. (AT(04-3)-326-PA 33) and the N.S.F. (GB 29094).
[2]Present address: Department of Human Genetics, Yale University School of Medicine, New Haven, Connecticut 06510.

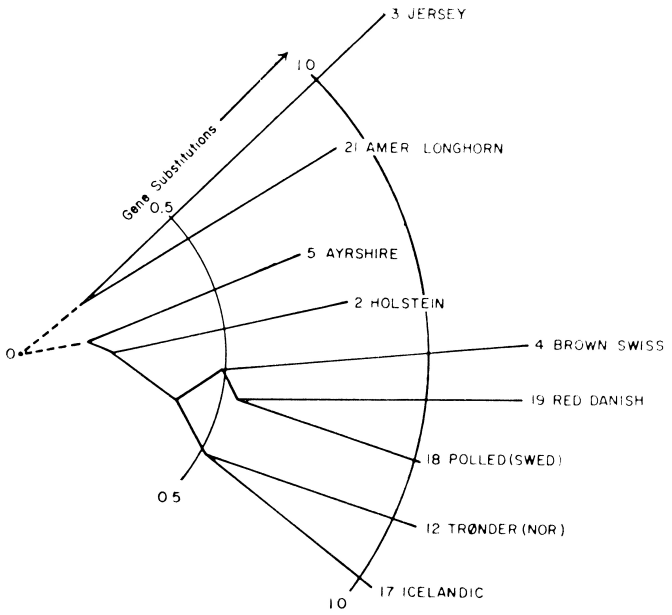

FIG. 1. A radial plot of an additive phylogenetic tree of nine European cattle breeds. This is the best fit to the data from among 122 different trees examined using distances from Kidd (1969) based on six loci. The reconstructed distances are plotted radially; the origin is arbitrarily placed in the center of the longest internal segment.

In spite of the apparent mixture in the human population, the cattle on Iceland seem unequivocally of Norwegian origin. Using the very informative *B* locus, Braend et al. (1964) found that Icelandic and Norwegian breeds have many alleles that are not found in any other breeds. A comparison by genetic distances based on six loci (Kidd, 1969) of data on Icelandic cattle with data on other European breeds has indicated that genetic distances are smaller between Icelandic cattle and Norwegian breeds than between these breeds and any of the other breeds studied. A tree reconstructed on that set of distances for nine cattle breeds is given in Figure 1. It shows the clear separation of the Norse breeds from the other Scandinavian breeds. A more recent study (Kidd and Sgaramella-Zonta, 1972) shows a great separation of Icelandic cattle from breeds of Great Britain, and specifically from the Angus cattle of Scotland. Thus, the results Of these analyses support the conclusion reached by earlier authors (see Braend, et al., 1962) that Icelandic cattle are totally derived from ancestral Norwegian cattle. The degree of separateness indicated for the Norse breeds (Figure 1) also supports the notion that the known importation of other breeds into Norway has had little effect on these gene frequencies in these old native Norwegian breeds.

POSSIBLE SELECTIVE FACTORS

Because of the potential value to agriculture, there have been concerted efforts to demonstrate major selective forces associated with the blood group loci and to find new polymorphic loci in which such associations might exist. Rendel (1967) surveyed the results of such studies and concluded that no strong associations had been demonstrated conclusively. Work done since that review has not altered this conclusion. Thus, we know of no selective forces that are likely to have resulted in a systematic gene frequency change at the loci used in this analysis.

There may, however, be many selective forces operating to maintain these polymorphisms. It is possible that the forces are too small to have been demonstrated with statistical significance in the tests and comparisons that have been made. The comparison of the observed amount of gene frequency change between the populations with that expected based on the time elapsed since their separation and on their demography may provide an indication of the existence of such forces. Should the polymorphisms be maintained by stabilizing selection, e.g., heterozygote advantage, we should find less difference than predicted on the basis of drift alone. If there are different selective forces operating in the different locations, we should find greater difference than predicted. However, selective forces are unlikely to be identical in nature for all loci and a test of heterogeneity of the variation at the various loci may be informative. On the hypothesis of drift alone, all loci should show the same amount of variation. On the hypothesis of selection, with different effects and intensities at various loci, we should expect that the variation at different loci is different (Cavalli-Sforza, 1966).

THEORY

Populations with constant size, N, breeding independently without cross migration over a lapse of t generations and in the absence of differential selection pressures, increase their diversity at a well known rate. An estimate of diversity is the variance of the frequency of one allele at a given locus, p_i, in the ith population among n populations. Assuming that at the beginning the populations had a homogeneous frequency, p_0, the variance V_t at time t is expected to increase with time as

$$V_t = \frac{\sum_{i=1}^{n}(p_i - \bar{p})^2}{n-1} \simeq p_0(1-p_0)(1-e^{-t/2N}) \quad (1)$$

while the mean gene frequency over all populations

$$\bar{p} = \frac{\sum p_i}{n} \quad (2)$$

is expected to remain constant and equal to p_0. Taking

$$\frac{V_t}{p_0(1-p_0)} \simeq \frac{V_t}{\bar{p}(1-\bar{p})} = f_t \quad (3)$$

as a measure of variation, which corresponds to F_{ST} in Wright's notation:

$$f_t \simeq 1 - e^{-t/2N} \quad (4)$$

The limiting value of $f_t(f_\infty)$ for $t = \infty$ is 1 where all populations are fixed for one allele or the other. If there is an outside constant source of genes with gene frequency $\hat{p}$, at a rate of m per generation (m being the proportion of individuals exchanged with the outside source), with m equal for all populations, then the exact asymptotic value is (Crow and Kimura, 1970)

$$f_\infty = \frac{V_\infty}{\hat{p}(1-\hat{p})} = \frac{1}{2N[1-(1-m)^2(1-1/2N)]}. \quad (5)$$

With several terms of the denominator usually negligible, this simplifies to the classical formula:

$$f_\infty = \frac{1}{1+4Nm}. \quad (6)$$

On the assumption that the original frequency in each subpopulation is equal to p0, the increase of f with time is (Feldman, pers. comm.)

$$f_t \simeq f_\infty\left[1-\left(1-\frac{1}{2Nf_\infty}\right)^t\right] \simeq f_\infty\left(1-e^{-t/(2Nf_\infty)}\right). \quad (7)$$

N must be estimated as effective population size, not census size. With cattle it is important to consider the effect of the sex ratio of reproducing individuals, which is different from 1:1. The harmonic mean of the numbers of reproducing animals in the two sexes, N_M and N_F, is used (Wright, 1931):

$$\frac{1}{N_h} = \frac{\frac{1}{N_M}+\frac{1}{N_F}}{2}. \quad (8)$$

Twice the harmonic mean of males and females, 2Nh, is the effective population size:

$$N_e = \frac{4N_MN_F}{N_M+N_F}. \quad (9)$$

The variation of N over generations is also accounted for by taking harmonic means. We have not considered the individual variation in progeny size, which, in times prior to artificial fertilization, is unlikely to be of great importance. In terms of the sex ratio among reproducing animals, $R = N_F/N_M$, and the proportion of reproductive animals in the population, $r = (N_M + N_F)/\bar{N}$ where $\bar{N}$ is the average (harmonic mean) census size, equation (9) becomes

$$N_e = \frac{4\bar{N}r\mathrm{R}}{(1+R)^2}. \quad (10)$$

Unbiassed estimates of V_t and of p do not necessarily give rise to an unbiassed estimate of f.

Moreover, the sampling properties of the statistic f are not known. A solution to this problem, which is satisfactory when the average gene frequencies are between .05 and .95, is to use, instead of gene frequencies, their angular transforms:

$$\theta = \sin^{-1}\sqrt{\mathrm{p}}. \qquad (11)$$

This, unlike the binomial variate, $p(1-p)/N$, has variance independent of p:

$$V_\theta \simeq \frac{1}{4N}. \qquad (12)$$

The variance of gene frequencies, V (given as a function of time in 1), is, by the standard formula for the variance of a function, transformed into

$$V_\theta \simeq \mathrm{v}\cdot\left(\frac{\mathrm{d}\theta}{\mathrm{d}p}\right)^2_{\mathrm{p}=\bar{\mathrm{p}}} \qquad (13)$$

where V_θ is the variance of the angular transformation. Given (11) and $\frac{\mathrm{d}\theta}{\mathrm{d}p} = \frac{1}{2\sqrt{p(1-p)}}$,

$$V_\theta \simeq \frac{V}{4\sin^2\theta\cos^2\theta} \qquad (14)$$

and hence

$$\frac{V}{\bar{p}(1-\bar{p})} = f \simeq 4V_\theta \qquad (15)$$

When only two populations are considered for one allele, θ_1 and θ_2 are the angular transforms of the gene frequencies p_1 and p_2, and $\theta_{12}=\theta_1-\theta_2$ is small, then

$$1-\cos\theta_{12} \simeq \frac{1}{2}{\theta_{12}}^2 = \frac{1}{2}(\theta_1-\theta_2)^2 =$$

$$\frac{\left[\theta_1-\frac{\theta_1+\theta_2}{2}\right]^2+\left[\theta_2-\frac{\theta_1+\theta_2}{2}\right]^2}{1} \qquad (16)$$

is an estimate of the variance $V_\theta = f_\theta/4$ for the population pair.

An interesting property of the angular transformation is that it makes the variance of θ effectively independent of the mean gene frequency, which does not appear in the formula for V_θ. Using equation (3), different expectations will be obtained when pairs of populations are compared depending on whether p is given as (a) the general mean of all populations or (b) the mean of only the two populations being considered. Using V_θ estimated by equation (16) this dichotomy disappears. Quantities proportional to $\sqrt{1-\cos\theta_{12}}$ have been used as measures of genetic distance (Cavalli-Sforza and Edwards, 1967) and the quantities proportional to f are on a squared scale with respect to distance.

With multiple allelic systems it is not entirely clear which weighting of the variances and/or covariances (see Nei, 1965) of gene frequencies is optimal. The angular transformation provides a practical solution (see, e.g., Edwards, 1971). One calculates the quantity

$$\theta_{12} = \cos^{-1}\sum_{i=1}^{k}\sqrt{p_{i1}p_{i2}}$$

where p_{i1}, p_{i2} are the frequencies of the ith allele in populations 1 and 2 respectively for a locus of k alleles. From unpublished work by Matousek (see also Bhattacharya, 1946) for samples of sizes N_1 and N_2 drawn from the same distribution

$$16(1-\cos\theta_{12})\Big/\left(\frac{1}{N_1}+\frac{1}{N_2}\right) \simeq$$

$$8{\theta_{12}}^2\Big/\left(\frac{1}{N_1}+\frac{1}{N_2}\right) \qquad (18)$$

is approximately distributed as χ^2 with degrees of freedom equal to the number of alleles minus one. An estimate of the variance $V_t/\bar{p}(1-\bar{p})$ for all k alleles at one locus can be obtained from equations (15), (16) and the above as

$$f_\theta = \frac{4(1-\cos\theta_{12})}{k-1}. \qquad (19)$$

The approximation is trivial if gene frequencies are in the prescribed range, and because of the independence of the sampling variance of θ on the p value, statistics based on it seem to provide to date the simplest answer to the problem of comparing gene frequencies for two or more populations. In addition, the test of heterogeneity between different loci is made easy by the angular transformation, since f_t values are now straight variances and the test

TABLE 1. *The gene frequencies used in this analysis are either taken directly from the references, are calculated from a Published frequency of the dominant phenotype, or are the pooled frequencies of several alleles here treated as one. The* A, C, *and* S *loci were all reduced to two alleles by considering only one antigen at each locus: A, C_1, and S_1. The* B *locus was reduced to four "alleles" defined by the three antigens B, G, and K, except that phenogroups with B and G but not K were included in "b". Sources: Icelandic (Braend et al., 1962), Telemark and Døla (Braend, 1959), Trønder (Braend, Berg, and Lie, 1964).*

Locus	Allele	Icelandic	Telemark	Døla	Trønder	Weighted average for Norway
A	*A*	0.276	0.196	0.243	0.083	0.203
	"*a*"	0.724	0.804	0.757	0.917	0.797
C	C_1	0.714	0.494	0.418	0.337	0.452
	"*c*"	0.286	0.506	0.582	0.663	0.548
F/V	*F*	0.994	0.9835	0.925	0.971	0.961
	V	0.006	0.0165	0.075	29	0.039
J	*J*	0.126	0.163	0.233	0.1	0.183
	j	0.874	0.837	0.767	0.9	0.817
L	*L*	0.341	0.426	0.166	0.301	0.32
	l	0.659	0.574	0.834	0.699	0.68
S	S_1 (*SH'*)	0.253	0.262	0.215	0.329	0.251
	"*s*"	0.747	0.738	0.785	0.671	0.749
Z	*Z*	0.337	0.489	0.308	0.231	0.4
	z	0.663	0.511	0.692	0.769	0.6
B	*BGK*	0.136	0.0587	0.0624	0.066	0.061
	B	0.137	0.1562	0.1777	0.099	0.159
	G	0	0.0242	0.0529	0.078	0.039
	"*b*"	0.727	0.761	0.707	0.757	0.741

of homogeneity of variances due to Bartlett can be applied.

An estimate of f can be obtained over several loci as the weighted average of the f values found at each locus:

$$\bar{f} = \frac{\sum_i (f_i (k_i - 1))}{\sum_i (k_i - 1)} \qquad (20)$$

where f_i and k_i are the f values and number of alleles for each locus. Substituting f_θ from equation (19) for f_i, this becomes

$$\bar{f}_\theta = \frac{4 \sum_i (1 - \cos\theta_i)}{\sum_i (k_i - 1)} \qquad (21)$$

For evolutionary analysis we want quantities that increase proportionately to time. With populations that evolve without migration, under drift alone, one obtains from (4):

$$\tau = -\log(1 - \bar{f}_\theta) \quad \simeq \quad -\log(1 - f_t) = \frac{t}{2N}. \qquad (22)$$

This is a suitable transformation of f which makes it equal to time in generations divided by twice the effective population size. When t and N_e are known, therefore, the expected value of f can be computed and compared with actual data.

ANALYSES

Observed Genetic Differences

Kidd (1971) calculated f values from the genetic distances used for Figure 1, but since we are now

TABLE 2A. *Summary of calculations of pairwise genetic differences.*

Locus	Breed comparisons	Iceland: Telemark	Iceland: Døla	Iceland: Trønder:	Iceland: Norwegian mean
		$1 - \cos\theta$ values per locus			
A		0.004462	0.000709	0.033841	0.003674
C		0.025685	0.045707	0.074020	0.036020
F/V		0.001314	0.019907	0.004376	0.007342
J		0.001389	0.009904	0.000846	0.003132
L		0.003829	0.020726	0.000918	0.000249
S		0.000053	0.001008	0.003511	0.000003
Z		0.011994	0.000481	0.006954	0.002135
B		0.020616	0.034900	0.046950	0.027360
			TABLE 2B		
$\Sigma(1-\cos\theta)$		0.069342	0.133342	0.171416	0.079915
$f_\theta \pm \sigma_f$		.028 ± .010	.053 ± .018	.069 ± .030	.032 ± .014
$\tau \pm \sigma_\tau$		.028 ± .010	.055 ± .019	.071 ± .032	.032 ± .015
χ^2_τ		7.35	4.53	7.92	12.57
		$p \simeq .4$	$.7 < p < .8$	$.3 < p < .4$	$.08 < p < .1$

* Bartlett's test for heterogeneity of the eight pairwise $1 - \cos\theta$ values in 2A.

limiting comparisons to the Norse breeds, additional loci can be included and thus more accurate values obtained. Table 1 gives the gene frequency data for eight loci that we extracted from the published reports. It also includes allelic frequencies for the weighted mean of the three Norwegian breeds, using the relative present breed sizes as the weights. The values in Table 1 are not the values reported for all systems since several of the loci involved are multi allelic factor union systems (Cotterman, 1969) that required special treatment. Since either the same antigens (factors) were not uniformly recognized in all studies or only factor frequencies, not allelic frequencies, were presented, three of these systems, the *A*, *C*, and *S* loci, were reduced to two allele systems defined by the presence vs. absence of one particular antigen, thereby allowing comparisons at these loci.

The *B* system presents similar problems, but overshadowing these is the presence of recombination within the system (Bouw and Fiorentini, 1971). The *B* system in cattle is the most complex blood group system known in any species: there are over 400 different phenogroups composed of various combinations of the more than 25 different antigens recognized in the system. Each phenogroup behaves as an allele in most cases in most pedigrees, but a significant number of recombinations producing new combinations of antigens (new phenogroups) have been observed. Such recombination would promote the formation of new "alleles", at the expense of existing "alleles", in excess of the frequency changes expected from genetic drift alone. It is therefore preferable to simplify this system if it is to be used in studies of genetic drift. We have chosen to reduce it to a four allele system defined by pooling together phenogroups that contain antigen B but not G, phenogroups that contain G but not B, those that contain B, G, and K, and finally those that have any other antigenic complement. This combination was chosen because the determinants of the antigens B and G appear closely linked genetically and because their joint occurrence on one chromosome is almost always accompanied by the production of the antigen K which is never produced otherwise. This treatment is recognized as a compromise between the desire to eliminate all recombination effects and the desire to obtain maximum information from this complex system. We feel this treatment should

Table 3. Comparison of three estimates of f *for two-allele loci for two breed comparisons. The gene frequencies used are given in Table 1. Though* f_θ *seems consistently larger than* σ^2/pq*, it is insignificantly different except when one allele in one population is rare,* $p < .05$*, as in the* F/V *locus in the Iceland:Døla comparison.*

	Locus						
	A	*C*	*F/V*	*J*	*L*	*S*	*Z*
Iceland : Døla							
f_θ	0.00284	0.18283	0.07963	0.03962	0.08290	0.00403	0.00193
θ^2	0.00284	0.18424	0.07989	0.03968	0.08319	0.00403	0.00193
f	0.00283	0.17834	0.06128	0.03887	0.08092	0.00403	0.00192
Telemark : Trønder							
f_θ	0.05524	0.05111	0.00326	0.01760	0.03396	0.01081	0.14817
θ^2	0.05537	0.05122	0.00326	0.01761	0.03401	0.01081	0.14909
f	0.05319	0.05075	0.00323	0.01738	0.03377	0.01078	0.14445

reduce effects of recombination to a negligible level while retaining much more information than if the system were reduced to a one antigen, presence vs. absence, locus.

Based on the data in Table 1, the $1 - \cos\theta$ values that were calculated for each locus for four different breed comparisons are presented in Table 2. The chi square values for Bartlett's test of heterogeneity of variances are not significant in any of the four comparisons. Details of the calculation of the f_θ and τ values are also presented in Table 2. Since these calculations were done, Lewontin and Krakauer (1973) have suggested a different test for the same purpose. Their test is based upon an estimate by computer simulation of the sampling distribution of f and is believed to give similar results.

Although almost all of the allelic frequencies in this study are in the range required by the angular transformation, f_θ (equation 19) and f (equation 15) were both calculated for the seven two allele loci. In most instances the agreement was quite good, but f_θ was virtually always the larger. Table 3 gives the two f values for two illustrative breed comparisons; θ^2 is also included. The greatest discrepancy occurs when, for one or both populations, one of the alleles is less than .05. In such cases, f_θ has been as much as 50% larger than f. For this reason we calculated two separate τ matrices, one based on f_θ (equation 21) and one using equation 20 to average the f values (equation 15) for the seven two allele systems and the f_θ value for the multiallelic system. These two τ matrices, with their standard errors, are given in Table 4. Two additional breeds, Hereford and Black Angus, are included in Table 4 using the data in Kidd (1969).

Though f and f_θ give slightly different results, at present it is difficult to choose between them. As already mentioned, it seems that f_θ is more appropriate for use in Bartlett's heterogeneity test. On the other hand, f_θ values average about 14% higher than f values. The regression of f on f_θ, using the data for the seven two allele systems in Table I for ten breeds including those in Table 4, is $f = .0047\ (\pm .0016) + .827\ (\pm .0089) \cdot f_\theta$. No single locus makes an exceptional contribution to this regression. Tables 2b, 4a, and 4b show that a difference of 14% is not important when compared with the standard error (between loci) which is % of the f value or greater; were the standard errors smaller, the difference might be more serious.

Both f and f_θ values are affected by a bias due to random sampling variance; neither value would be zero, even if computed on different samples from the same population. For f_θ, the expected bias can be computed from the Bhattacharya-Matousek distribution to be $(N_1 + N_2)/4N_1N_2$, where N_1 and N_2 are the sample sizes. In our case, the sample sizes for the Norse breeds were of the order of 1000. Thus, the sampling biases were of trivial magnitude and corrections were not applied.

TABLE 4A. *Matrices of τ values. The τ values are in the lower triangular matrix, their respective standard errors in the upper triangular matrix. (A) The matrix using* f_θ *values. (B) The matrix using* f *values, instead of* f_θ, *for all two allele systems. See text for additional explanation.*

		1	2	3	4	5	6	7
Iceland	1	0	0.0103	0.0191	0.0322	0.0145	0.0567	0.0553
Telemark	2	0.0281	0	0.0181	0.0149	0.0028	0.0641	0.0448
Døla	3	0.0549	0.0341	0	0.0105	0.0067	0.0807	0.0301
Trønder	4	0.0710	0.0371	0.0337	0	0.0081	0.1202	0.0760
Norway mean	5	0.0325	0.0059	0.0120	0.0233	0	0.0646	0.0393
Hereford	6	0.1771	0.1884	0.2124	0.2811	0.1916	0	0.0658
Black Angus	7	0.2158	0.1656	0.0851	0.1722	0.1237	0.1327	0
		1	2	3	4	5	6	7

TABLE 4B

		1	2	3	4	5	6	7
Iceland	1	0	0.0101	0.0182	0.0306	0.0141	0.0399	0.0380
Telemark	2	0.0279	0	0.0173	0.0145	0.0027	0.0470	0.0318
Døla	3	0.0522	0.0329	0	0.0099	0.0066	0.0683	0.0248
Trønder	4	0.0686	0.0364	0.0327	0	0.0079	0.0898	0.0601
Norway mean	5	0.0317	0.0059	0.0118	0.0229	0	0.0496	0.0307
Hereford	6	0.1477	0.1597	0.1863	0.2312	0.1656	0	0.0606
Black Angus	7	0.1866	0.1443	0.0771	0.1442	0.1099	0.1262	0
		1	2	3	4	5	6	7

Expected Genetic Divergence Under Drift

We shall estimate $t/2N_e$, separately for Icelandic cattle and Norwegian cattle based on the 1,000 years since separation. The expected values separating the two modern contemporary populations will then be the sum of two values, one to each population from the common ancestor. The formula used to calculate $t/2N_e$ from certain demographic parameters is given earlier. The following sections explain our estimates for these parameters. The calculations are summarized in Table 5.

TABLE 5. *Calculation of expected 7 values using demographic estimates.*

Breed	$\bar{N}$	N_e[1]	$t/2N_e$
Iceland	27,500	5,858	.0213
Norway (total)	250,000–300,000	≃ 58,500	.0021
Telemark	?	?	?
Døla	25,200	5,370	.0233
Trønder	14,500	3,096	.0404
Breeds being compared		τ expected[2]	τ observed[3]
Iceland : Norway (Total)		.023	.032 ± .015
Iceland : Telemark		.0213 + ?	.028 ± .010
Iceland : Døla		.045	.055 ± .019
Iceland : Trønder		.062	.071 ± .032

[1] $N_e = \frac{4rR}{(1+R)^2} \cdot \bar{N} = \frac{4(.75)(12)}{(1+12)^2} \cdot \bar{N} = .213\bar{N}$

[2] τ expected is $\frac{t}{2N_e}$ Iceland + $\frac{t}{2N_e}$ Norwegian breed

[3] τ observed is taken from Table 2B.

Total Population Size

The cattle population in Iceland varied considerably in the millennium since colonization. Braend et al., (1962) offer the following summary:

". . . In the 13th Century the cattle population is assumed to have exceeded 100,000 animals . . . During the period of general decline which followed thereafter the cattle population decreased considerably. It amounted to 35,800 animals in 1703 and was further reduced to 9,800 after the volcanic eruptions in 1783–1784. Today the number of cattle in Iceland is about 53,000."

The effect of variation in population size can be dealt with by taking the harmonic mean of population sizes at every generation. Using the above summary, one gross approximation would be that there were 100,000 cattle for 2/10 of the period, 10,000 for 2/10 of the period (to account for both the post-eruption period and an initial period during which the number may have been small) and 50,000 for the remaining 6/10. This gives a harmonic mean of 29,400. These seem to be maximal estimates of size, and a smaller, more nearly minimal estimate might be 100,000 for 1/10, 10,000 for 2/10, and 40,000 for 7/10. These values give 26,000 as the harmonic mean. For our calculations we shall take an intermediate value of 27,500.

The cattle population in Norway has shown a steady increase since the first census in 1657 when there were 450,936. In subsequent censuses, the cattle population was 524,900 (1723), 856,380 (1819), 949,940 (1855) and 1,343,245 (1938). Estimates before 1657 are rough. Assuming that before the plague came to Norway in 1349, there were about 50,000 farms with an average of 6 cattle each, there were about 300,000 cattle. This number must have decreased somewhat as a consequence of the plague, and was probably smaller during the preceding centuries as well. Making a slight allowance for the imported cattle breeds which contribute significantly to the cattle census in the last two centuries, the harmonic mean for total cattle in Norway is between 250,000 and 300,000; we used 275,000.

In the 1657 census, there were 30,111 cattle in the Døla region, 18,18l in the Trønder region, and 7,792 in the Telemark region. French, et al. (1966) report that about 1960 there were slightly less than 40,000 cattle in the Trønder breed, about 160,000 cattle in the Døla breed, and about 235,000 cattle in the Telemark. Thus, on these figures, the Trønder appears to have remained relatively stable at 4% (1657) to 3% (1960) the Døla to have increased from 6% (1657) to 12% (1961) ; and the Telemark to have increased from less than 2% (1657) to 18% (1960). The data for this last breed are probably incomplete, since it seems unlikely that a breed as large, popular and phenotypically varied as the Telemark breed during the late 19th and early 20th centuries was developed from only 8,000 animals in 1657. In fact, French, et al. (1966) imply that cattle from districts adjacent to Telemark were involved in the formation of the breed.

For simplicity, we assumed the average number of cattle in each breed for the period 950–1450 to be 2/3 of the 1657 number, the average from 1450–1650 to be 5/6 of the 1657 number. The period 1650–1950 was broken into 100 year intervals and the percentage in each breed estimated by interpolation for 1750 and 1850. The number was then estimated as that percentage of the total. For the harmonic mean, the number at the beginning of each 100 year period was used for the entire period. This makes little difference except during the period 1750–1950, but during the last half of this period, the sex ratio changed, so that by using the lower 1750 and 1850 values, we approximately offset the sex ratio change. Thus, a rough harmonic mean for Døla is 25,000 and for Trønder is 14,500. Until we obtain additional historical data on its origins, such a calculation seems unjustified for the Telemark breed.

Sex Ratio

We do not have direct information about early sex ratio for Norwegian cattle, but do have some indirect data from the late 19th century. According to the *Norwegian Agricultural Yearbook* for 1877, one Norwegian herd in 1876 had 30 cows, 3 bulls, and 8 young animals. In local shows in the same year in Christiania, total cattle shown were 2200 cows, 465 heifers, and 150 bulls. The *Yearbook* for the following year states that in Telemark 432 cows, 133 heifers, and 56 bulls were shown. In another series of local shows supported by the government there were 1746 cows, 317 heifers, and 157 bulls. For cows to bulls, these figures give 10:1, 14.7:1, 7.7:1, and 13.2:1 and 11.1:1. Because only the larger farms in the neighborhoods kept bulls, which were then used by the smaller farms, it is likely that the first ratio is an overestimate of the proportion of males since it is only one farm. The other ratios are probably biassed since these are animals shown in "county fairs," not the total resident population. Unfortunately, it is not possible to state for certain either the direction or magnitude of any resulting bias, although it seems likely to us that bulls might be slightly favored. Treating all numbers together, we get a ratio of 12.1:1.

Our calculations have been made assuming 12:1 as the sex ratio because greater numerical accuracy is not warranted at this time and because the above are the data most likely to be representative of the whole 1000 year period we are considering. That this may be an underestimate is suggested in data presented by Thorsteinsson (1946) for Icelandic cattle between 1890 and 1945. There is a twofold increase in the sex ratio between 1900 and 1945, going from approximately 15 in 1900 to over 30 by 1945. Since no data have been found to indicate whether this trend may have begun before 1890, we use the earlier estimate from Norway for both populations. While it may be an underestimate, it could not be off by far.

Proportion, of Reproducing Animals

The preceding figures from Norwegian cattle show that about 18% (unweighted average of five estimates) of the population are pre-reproductive animals. However, here it is easy to see that this must be an underestimate since young calves would not usually be taken to shows, and indeed, no calves or steers are listed in the tabulations. A truer estimate should be higher, and, indeed, Thorsteinsson's data on Icelandic cattle show that from 1890 to 1945 an almost constant fraction of 25% of the population was pre-reproductive. Therefore, we have used 0.75 as the fraction of reproductive animals.

Average Number of Generations

Cattle husbandry practices probably did not change much during most of the time interval considered. While the age at first calving has decreased from nearly three years to closer to two years during the last hundred or so years (Hogstad and Trodahl, pers. comm.), it is not likely that this trend could be extrapolated further back in time. Norwegian husbandry practices (Hogstad and Trodahl, pers. comm.) have been to keep a cow for a very long time, during which she would produce many calves. A reasonable estimate of the average generation length would therefore be around five years. However, the males began reproducing at about 1½ years of age and had usually finished reproducing by the age of four years.

This difference in reproductive lifespans between the sexes would properly be incorporated into the calculations by weighting the numbers of each sex by the inverse of their reproductive period. We choose, however, to simply use an intermediate value of four years for the average generation length. This makes little difference in these calculations at the present level of approximations.

Calculations of Expected Divergence

We assume that all demographic parameters except total population size are the same for

cattle in Iceland and Norway. We have made two alternative assumptions: that each of the three Norwegian breeds is an evolutionarily separate population with respect to Iceland or that there has been sufficient migration during most of the period that the total cattle population in Norway should be considered the evolutionary unit. Reality probably lies between these extremes. Table 5 summarizes the calculations on these two assumptions and gives the results.

DISCUSSION

The values in Table 2 for four different breed comparisons are homogeneous over the eight loci. Thus, we have no evidence for selection acting differentially at these eight loci. This, in itself, is a strong argument for the observed differences being entirely due to chance, since selection is unlikely to operate similarly at all eight loci, with the possible exception of stabilizing selection. The strength of this argument is weakened, however, by the fact that a test of heterogeneity of variances has low statistical power. To test further the hypothesis that drift alone is responsible for the observed divergence, it is necessary to compare this observed difference with that expected on the basis of the histories and demography of the populations.

In Table 5 we have compared the expected divergences τ computed from demographic data alone with that observed from genetic data. The agreement is close. Thus, within the margin of error of these analyses, random genetic drift appears sufficient to account for the observed differences between Icelandic and Norwegian cattle. Both the homogeneity of the variation at these eight loci, and the absolute magnitude of the differences support this conclusion. Our alternative assumptions on the degree of isolation of the breeds in Norway have not led to significant disagreement in either case. Also, we note that the observed variation is slightly greater than that expected in all three comparisons, though this might not hold for the Telemark, had we adequate historical data.

Any firm conclusion must consider the precision of these calculations. The standard errors of the observed τ values (Table 4) are large, as expected for a variance. Additional genetic data are obviously desirable. Inclusion of additional loci and additional allelic subdivisions could have two possible effects: the reduction of the standard errors of the τ values and/or the detection of heterogeneity among the larger number of f values. Both of these might suggest that our present conclusion is wrong and that selective forces have operated in the divergence of these breeds.

While no measure of reliability is possible for the demographic parameters, their precision obviously affects our confidence in any conclusion. Therefore, we have calculated the effect of individual variation of each parameter over its reasonable limits. Table 6 shows these limits and the percentage change each would make in the expected τ value. The standard errors of the observed values with which the "expected" τ values are to be compared (see Table 5) are about 36% (Icelandic-Telemark), 35% (Icelandic-Døla), 45% (Icelandic-Trønder), and 45% (lcelandic-Norway mean) of their respective observed means over loci. It will be noted that the change in the expected values determined by variations in the parameters T, R, r, and N are almost always within one standard error. They cannot therefore be individually responsible for significant departures between observed and expected. Perhaps the single most important source of error is in the variation of R, the sex ratio, judging from the percentages in Table 6. If more than one of the estimates of T, R, r, and for the N's are wrong, in most combinations the errors would tend to cancel out because of the reciprocal relationship. Only if several estimates happen to be wrong in directions such as to increase the departure, does a significant discrepancy between observed and expected τ values remain a possibility.

TABLE 6. *Range of errors in expected τ values.*

The expected τ values will change on average with respect to that indicated in Table 5	
from + 33% to – 20%	if T, the generation time, is respectively 3 to 5 years (instead of being 4 years)
from – 29% to + 57%	if R, the ratio of females to males, is respectively 8:1 to 20:1 (instead of being 12:1)
from + 15% to – 12%	if r, the proportion of reproductive animals in the herd, is .65 or .85 (instead of being .75)
from + 37% to – 31%	if $\bar{N}$, for Icelandic cattle, is 20,000 or 40,000 (instead of 27,500)
from + 37% to – 31%	if $\bar{N}$, for all Norwegian cattle is 200,000 or 400,000 (instead of $\simeq$ 275,000)
from + 26% to – 16%	if $\bar{N}$, for the Døla breed is 20,000 or 30,000 (instead of 25,200)
from + 45% to – 27%	if $\bar{N}$, for the Trønder breed, is 10,000 or 20,000 (instead of 14,500)

Suggestions as to the most likely direction of error for most parameters are possible. While the average generation length may have been longer than 4 years, it is unlikely to have been much shorter. The sex ratio in Iceland around 1900 was 15, suggesting that 12 is an underestimate. Because of possible bottlenecks in the period before 1657 and the contribution of imported cattle to the census size, the effective number of pure Norwegian cattle could be less than we calculated. Also, because of the selection used to standardize the Norwegian breeds during the last century, the effective size of each breed may have been overestimated. The proportion of reproductive animals and the census size on Iceland seem sufficiently accurate to be ignored for the moment. Thus, though possibly moderated by a longer generation length, the combined effect of a higher sex ratio and smaller Norwegian population could lead to a significant difference between observed and expected. This possibility cannot be discounted from the present data. However, there is one factor, migration among the Norwegian breeds, that could counter balance a smaller population size, as discussed below.

In addition to errors in our demographic and genetic data, relationships among the Norwegian breeds deserve consideration. The comparisons in this paper have been possible because it is reasonably certain that there has been no migration between Norway and Iceland after the original colonization period. The analyses done either assumed that each of the four breeds has been completely isolated and independent since their separation 1000 years ago or that all cattle within Norway behaved as one unit because of migration. In fact, one expects that breeds in geographical proximity would exchange some genes. Thus, the Norwegian breeds may not have been completely isolated. In addition, Norwegian breeds may have separated from each other at times different from the Icelandic-Norwegian split. The greater similarity among Norwegian breeds than between some breeds and Icelandic cattle can be explained by assuming either that the Norwegian breeds separated after the Norwegian Iceland split, or, more probably, that they separated earlier, but with migration among them damping their divergence.

Equation 7 is the appropriate equation for such a situation, but additional unknowns – such as migration rate and times of separation within Norway – must be considered. We do not have appropriate data for this. Instead, the two extremes of no migration and of migrational equilibrium will be briefly considered. In the latter case we can use equation 6 and obtain an estimated migration rate of between 1 and 2 per thousand

per generation among Norwegian breeds, assuming N_e for the average breed to be 4,000 to 5,000. There would then be roughly 10 such subdivisions with nearly 10 migrants entering each breed per generation. This is a number large enough that subdivision becomes negligible and the population evolves as a whole (Moran, 1962). The alternative extreme view is that the Norwegian breeds have diverged since the separation of Icelandic cattle and there is no migration. The observed τ value estimates $t/2N_1 + t/2N_2$ for two breeds separated t generations. Using this relationship, the estimate of effective population size in Table 5 and the observed difference between Døla and Trønder (Table 4), we calculate a separation time of 132 generations.

A very small amount of migration is seen to be sufficient to produce the observed f value at equilibrium. In simulations, populations of this size with migration of this magnitude were close to the equilibrium f value after 400 generations, a time interval not grossly different from that considered here. Alternatively, in the absence of migration, even the most recent breed separation would have occurred over 100 generations ago. Until additional historical data are found, both the "static equilibrium" and "dynamic drift" views remain tenable.

These analyses demonstrate the use of demographic ("bosographic"), historical, and genetic data in an attempt to test for the existence of selective pressures at polymorphic loci and, if found, to measure their relative intensities. Although their possible existence cannot be excluded, no evidence was found for the presence of selective forces at the loci studied: random genetic drift would be sufficient to account for the observed differences. However, the facility with which the breed relationships within Norway can be successfully treated either as an equilibrium situation or as an ongoing evolutionary divergence emphasizes the need for additional data at all levels. Because of the current emotionalism in the selection vs. drift controversy, it is probably worth emphasizing that these results only apply to differences between Norway and Iceland. While there are some climatic and other environmental and husbandry differences, these are probably small compared with differences between Norse and, say, Southern European environments. These results suggest the absence of selective forces acting on eight particular loci during the past millennium in four specific breeds in Iceland and Norway. This conclusion cannot be extrapolated with any confidence. Moreover, our recognition of only certain antigenic factors at several loci (necessary for the comparison) has reduced the possibility of detecting selective advantage and/or disadvantage associated with other antigenic factors. Nonetheless, we find the close agreement found between the observed and expected divergence quite remarkable.

Both better estimates of the demographic parameters at different periods of time and gene frequency data for additional polymorphic systems will be essential for a more detailed analysis.

Additional genetic data are possible. There are now over 25 polymorphic loci known in European cattle, and many of the newer additional loci are probably polymorphic in these breeds too, although at least one, hemoglobin is known to be fixed in all Northern European breeds, including these four. In fact, in cooperation with Prof. W. H. Stone, Laboratory of Genetics, University of Wisconsin, Madison, and Petur Gunnarsson, Director, Agricultural Society of Iceland, additional genetic data on Icelandic cattle has already been collected (Kidd, 1969). When information is obtained for these same newer systems in the Norwegian breeds, the genetic comparisons can be improved. There is one major obstacle to such studies, however: these breeds of Norwegian cattle are being cross bred to other types to improve their production; in the process the potential for this type of analysis is being rapidly eliminated. Because of the potential for identifying loci of selective importance, we hope it will be possible to

thoroughly study these Norwegian cattle for the new genetic markers before hybridity becomes universal.

SUMMARY

On the assumption of random genetic drift, the mathematical relationship between gene frequency differences among populations and the demography and history of those populations has been derived. The types of demographic data needed for such studies are discussed and specific estimates made for Icelandic and Norwegian cattle breeds, which represent a unique historical situation. Analysis of genetic and demographic data on Icelandic cattle and on three Norwegian cattle breeds showed that random genetic drift alone was sufficient to account for the observed differences; no evidence of selective forces was found. Additional genetic and demographic data are needed to strengthen this conclusion; both can be collected, but the genetic data must be collected before hybridization swamps the Norwegian breeds.

ACKNOWLEDGMENTS

We wish to thank Dr. M. Braend for his critical comments on an earlier draft of this paper and for his efforts in obtaining demographic data. We also wish to thank Dr. Halldis Lie for her hospitality and assistance on the occasion of a brief visit to Oslo by K. K. K.

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