

THE USE OF THE GENETIC DISTANCE BETWEEN CATTLE BREEDS
TO PREDICT THE HETEROSIS IN CROSSES

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Introduction

The large number of cattle breeds which exist throughout the world represents an important resource for cattle breeding. However the very richness of this resource makes it impossible to compare all possible breeds and crosses in field experiments. Therefore a method of predicting the performance of different genotypes would be very useful.

According to the theory of quantitative genetics heterosis is simply the recovery of the inbreeding depression that has occurred in each breed since the breeds have been separated. The amount of inbreeding can be estimated from the gene frequencies at neutral loci and the inbreeding depression per per cent inbreeding is known from experiments on inbreeding.

In this paper we use published data on heterosis, inbreeding depression and gene frequencies to test the hypothesis that heterosis can be predicted in this way.

Theory

Provided there is no epistasis, inbreeding depression within a breed is proportional to the inbreeding co-efficient F , where

$$F = \frac{H_P - H_I}{H_P}$$

and H_P = heterozygosity of the outbred parent population

H_I = heterozygosity of the inbred animals

Similarly the heterosis in a cross should be proportional to the increase in heterozygosity (F') where

$$F' = \frac{H_{F_1} - H_{\bar{P}}}{H_{\bar{P}}}$$

where $H_{\bar{P}}$ is the mean heterozygosity in the parent breed and H_{F_1} is the heterozygosity of the F_1 cross. Expressing both increases and decreases in heterozygosity relative to the heterozygosity in the parent breeds is based on the assumption that a 1% increase in H has the same effect, although in the opposite direction, to a 1% decrease in H .

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F' can be calculated from F_{ST} which Kidd et al (1974) used to measure the distance between breeds by

$$F' = \frac{F_{ST}}{1 - F_{ST}/2} \quad (1)$$

Materials and Methods

F' values: We have used two sources of data to calculate F' between cattle breeds. Firstly Kidd et al (1974) have published F_{ST} or the very similar F_{θ} values for several breeds based on blood group and protein loci. Formula (1) has been used to calculate F' for these breeds. Secondly Baker and Manwell (1980) published average gene frequencies at protein loci for groups of breeds such as Pied lowland, Indian zebu. We have used these to calculate F_{ST} values and then F' values by formula (1).

Heterosis: Data on weaning and yearling weights and calving rate were taken from the experimental results tabulated by Long (1980) and from Crockett et al (1978 a and b), Long et al (1979 a and b), Peacock et al (1981), Willham et al (1973), Koger (1973), Sacker et al (1971), Dillard et al (1980), Peacock and Koger (1980), Thorpe et al (1980 a and b), Tawgnezu et al (1980). Data on milk yields was derived from Okumu and Berry (1966) since this experiment used a much larger number of animals than other published experiments. For weaning weight, yearling weight and milk yield heterosis (mean of F_1 s minus mean of purebreds) has been expressed as a percentage of the parental mean. Heterosis for calving rate (mean F_1 cows minus purebred cows) has not been expressed as a percentage of the parental mean but simply in % units.

Inbreeding depression: Published results on the effect of inbreeding within a breed for weaning weight, yearling weight, milk yield and calving or conception rate as a trait of the cow have been collected and the inbreeding depression expressed in the same units as described for heterosis. The average of the values obtained are given in Table 2. (Complete references for the estimates of inbreeding and heterosis are available from the authors).

Statistical analysis: For each dependant variable two analyses were performed, one using all the data and one using only the data on crosses among Bos taurus breeds. (For milk yield all data is on B. taurus crosses). The simplest theory would predict that the relationship between heterosis (y) and F' would be a straight line through the origin. To test this the following models were fitted using least squares:

$$\begin{aligned} y &= a & (1) \\ y &= a + bF' & (2) \\ y &= bF' & (3) \end{aligned}$$

The difference in error SS between model (1) and (2) is the SS due to the slope of the regression and the difference in error SS from models (2) and (3) is used to test the significance of the intercept. Both these effects are tested over the error MS from model (2).

However if selection acts on the loci causing heterosis, the relationship between heterosis and F' may be non-linear. Two further models were fitted by least squares to test this:

$$y = A(1 - e^{-KF'}) + C \quad (4)$$

$$y = A(1 - e^{-KF'}) \quad (5)$$

The difference in error SS between models (4) and (2) tests for non-linearity of the regression and the difference between the error SS from model (4) and (5) tests the significance of the intercept in the non-linear model. These SS are compared with the error MS from model (4).

Results

F' values: The F' values calculated from Kidd et al (1974) and Baker and Manwell (1980) are given in Table 1.

Table 1: Genetic distances (F') between cattle breeds

Cross	% F'(1)	% F'(2)	Cross	% F'(1)	% F'(2)
⁺ H - A	23.1		H,A,S - B		106.7
H - Ho	19.3	} 5.0	R - Bo		42.7
A - Ho	9.1		Sx - Af		33.2
Ayr - Ho		} 26.8	Ho - J	16.8	17.0
H - J	28.8		Ho - G	8.0	7.5
A - J	23.7		Ho - Bs	11.4	8.3
Ayr - J		17.0	Ho - B		94.3
Ayr - G			J - G	14.8	
H - Bs	24.2	} 19.5	J - B		61.8
A - Bs	14.0		C - B		67.4
H - C	20.9	} 19.4	B - Af		33.8
A - C	13.0		An - Ba		5.5
			Bo - Ba		5.5

(1) F' values derived from Kidd et al (1974)

(2) F' values derived from Baker and Manwell (1980)

+H = Hereford, A = Angus, S = Shorthorn, Ho = Holstein/Friesian,
 Ayr = Ayrshire, J = Jersey, G = Guernsey, Bs = Brown Swiss
 C = Charolais, B = Brahman, R = Red Poll, Bo = Boran, Sx = Sussex,
 Af = Africander, An = Angoni, Ba = Barotse

The F' distances between individual breeds should be greater than the F' distances between groups of breeds due to the divergence of breeds away from their group mean. This is most noticeable for the Hereford but for other distances there is reasonable agreement between the two data sets. The high values for distances involving the Hereford are not surprising because there was considerable inbreeding during the formation of this breed, as there was in the formation of the Shorthorn breed (Wright 1977). This suggests that most breeds have not diverged far from the rest of their group. This was confirmed for Norwegian breeds by Kidd and Cavalli-Sforza (1974) who found F_0 amongst Norwegian breeds to be approximately 3%. Therefore for the statistical analyses, F' distances from Kidd et al (1974) were used wherever they were available. For other distances between breeds within a group a value of 3% was used except for Shorthorn-Angus and Shorthorn-Hereford which were given the same value as Hereford-Angus (23%). For distances between groups, F' values calculated from Baker and Manwell were used except that the distance between Sanga breeds (Mashona, Barotse) and African zebu breeds (Angoni and Boran) was increased by 3.0% to 8.5% to allow for divergence from group mean and the Ayrshire-Holstein distance was increased to 6.1%.

Relationship of Heterosis to F': The analysis of variance within the B. taurus crosses showed that the linear effect of F' was significant for yearling weight and weaning weight while the intercept and departure from linearity were not significant for any trait. When all crosses are included in the analysis the non-linear model (4) gives a significantly better fit to the data than the linear model (2) for yearling weight and there is a similar trend in weaning weight and calving rate. The intercept in the non-linear model was not significant for any trait. In fact for each trait model 5 gave the lowest error

MS for the analysis of the complete data and model 3 for the analysis of the B. taurus crosses alone. The regression co-efficients and the standard errors for these models are given in Table 2. For the analysis of the complete data with model 5, AK is also given since this is the slope of the line at the origin and therefore can be directly compared with the linear regression from model 3.

Table 2: Least-squares constants and effect of inbreeding

	Inbreeding depression	<u>B. taurus</u> crosses [†] b (se)	A (se)	All data [‡] K (se)	AK
Yearling weight	.32	.29 (.026)	16.7 (2.9)	.025 (.007)	.42
Weaning weight	.25	.21 (.013)	26.1 (9.9)	.010 (.005)	.25
Calving rate	.50	.18 (.049)	9.2 (2.0)	.025 (.014)	.23
Milk yield	.44	.25 (.054)			

† Constants based on model 3 $y = bF'$
[‡] Constants based on model 5 $y = A(1 - e^{-KF'})$
 Heterosis (y) and F' both measured in %

Discussion

The results show that the genetic distance F' estimated from gene frequencies is useful in predicting the heterosis obtained in crosses. The deviations from the regression lines are large but this is to be expected given the errors in measuring both heterosis and F'. The curvilinear nature of the regression is due to the lower heterosis/%F' in B. taurus x Brahman crosses than in crosses among B. taurus breeds.

Natural and artificial selection during the evolution of present day cattle breeds would have opposed the dispersive effects of inbreeding on gene frequencies at loci causing heterosis. Selection is most effective in this regard if the selection co-efficients and the effective population size (N_e) are large. For yearling and weaning weights the heterosis/%F' in crosses among B. taurus breeds is in good agreement with the estimates of inbreeding depression suggesting that selection has had little effect. However for B. taurus x Brahman crosses and for calving rate and milk yield the heterosis is less than expected from the inbreeding depression (Table 2). This can be explained by assuming that the divergence of the B. taurus from B. indicus breeds occurred at a higher N_e than the divergence among the B. taurus breeds, and that the selection co-efficients for calving rate and milk yield are higher than those for weight.

SUMMARY

The number of cattle breeds available throughout the world for cross-breeding is so great that it is impossible to compare all possible crosses in field experiments. Furthermore, these experiments are very costly to perform. Therefore, a method of predicting the most promising crosses would be very useful. The heterosis which occurs in a cross is proportional to the inbreeding that has occurred within each of the breeds since they diverged. This inbreeding or genetic distance can be estimated from the gene frequencies at blood group and protein loci. This paper tests the hypothesis that this genetic distance can be used to predict the amount of heterosis which occurs.

Published data on heterosis for weaning weight, yearling weight, milk yield and calving rate were used. In all four traits heterosis was positively correlated with genetic distance. For the two weights the heterosis per % inbreeding was in good agreement with published estimates of inbreeding depression. For milk yield and calving rate the heterosis was less than expected from estimates of inbreeding depression. The reasons for this are discussed.

R E S U M E N

El número de razas de vacuno disponible en el mundo para cruzamiento es tan grande que es posible comparar todos los posibles cruces en experimentos de campo. Además, estos experimentos son muy costosos de realizar. No obstante, podría ser utilizado un método de predicción para los cruces más prometedores. La heterosis que sobreviene en un cruce es proporcional a la consanguinidad que ha sobrevenido dentro de cada una de las razas desde que incidieron unas en otras. Esta consanguinidad o ~~genética~~ distancia genética puede estimarse a partir de las frecuencias génicas en los grupos sanguíneos y ~~loci~~ loci proteínicos. Este trabajo estudia la hipótesis de que esta distancia genética puede utilizarse para predecir la cantidad de heterosis que sobreviene. Se utilizan datos publicados sobre heterosis para los pesos al destete, pesos al año, producción lechera y producción de terneros. En los cuatro caracteres, la heterosis estuvo positivamente correlacionada con la distancia genética. Para los dos pesos, la heterosis por consanguinidad por 100 ~~loci~~ estuvo en un buen acuerdo con las estimaciones publicadas sobre depresión de consanguinidad. Para la producción de leche y la producción de terneros, la heterosis es menor que la esperada de las estimaciones de la depresión por consanguinidad. Se discuten las razones existentes para ello.

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