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GENETIC PARAMETERS OF BRITISH LARGE WHITE BACON PIGS

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THE advent of pig progeny testing on a national scale in Britain has made it possible to study the genetic parameters of British pigs tested under carefully controlled conditions with individual feeding. This paper presents estimates of heritabilities and genetic correlations among 35 measurements and scores of Large White pigs. To investigate the inter-relationships of the large number of items studied, a principal component analysis was carried out on the correlation matrices obtained.

MATERIAL AND METHODS

For this analysis data from 494 Large White litter groups tested at the National Progeny Testing Stations during the period from autumn 1957 to spring 1959 were used. Only balanced litter groups of two castrated males (hogs) and two females (gilts) with complete records were included. Pigs entered the stations at 30–45 lb. live-weight, the four pigs comprising the litter group being within a weight range of 8 lb. The pigs were fed individually by hand to appetite, starting the test at 50 lb. live-weight, when they were slaughtered on the following day.

Results were not released to the breeder until four litter groups per sire had been tested, but the data here involved 52 sires with four groups, 40 sires with three groups, 58 sires with two groups and 50 sires with one group. The loss of data from 20 pairs of gilts, due to computer failure, made the distribution of sires and degrees of freedom throughout slightly different for the two sexes. Sexes were analysed separately.

The five stations provided 25, 20, 15, 27 and 13% of the data respectively, and three consecutive six-month periods 25, 32 and 43%. To each pig, 'dummy' variables (0 if absent, 1 if present) were assigned for four stations and two periods (e.g. Quenouille, 1950). The sums of squares and crossproducts (S.S.P.) of each source of variation could then be corrected for differences due to stations, periods and last live-weight (all fixed effects) by multiple regression. This is equivalent to the method of fitting additive constants, adjusting the original data by these constants (irrespective of statistical significance) and then analysing the adjusted data. A hierarchical analysis, between sires, between litters within sires, and within litters was performed. The expected mean squares are not changed by adjusting the data for fixed effects.

The work was done by the Elliott-N.R.D.C. 401 computer at Rothamsted.

Three programmes were written, one using ordinary arithmetic for betweenand within-litter S.S.P., one using floating point arithmetic for (weighted) between-sires S.S.P. and one, floating point, for matrix addition, scalar multiplication and elimination by regression of 'dummy' variables for seasons and stations. The first programme, when accumulating betweenlitters S.S.P., subtracted working means from the observations to avoid overflow and to maintain accuracy, and punched out the means for each sire on tape. This tape was then used as a data tape for the between-sires S.S.P. Various data-reading and numerical checks were employed. The floating point arithmetic works to about seven decimal places, so that the final results are arithmetically correct to at least three decimal places.

The distribution of additive genetic variance among the various components of variation was calculated in the manner described by Dickerson (1947). The genetic relationships (Wright, 1922) required were obtained from a slightly different sample of 60 sires, all with four litter groups tested. The average relationship between sows mated to one sire was 0.096 and between a sire and his mates 0.042. The expected mean squares and the composition of the components of variance and covariance are:

	d.f.	Expected mean squares	Composition of components
Between sires	199	$\sigma_1^2 + 2\sigma_2^2 + 4.935\sigma_3^2$	$\sigma_3^2 = 0.295 \sigma_G^2$
Between litters within sires	288	$\sigma_1^2 + 2\sigma_2^2$	$\sigma_2^2 = 0.226\sigma_G^2 + \sigma_L^2$
Within litters	493	σ_1^2	$\sigma_1^2 = \sigma_E^2 + 0.479\sigma_G^2$

where σ_G^2 , σ_L^2 and σ_E^2 represent respectively the additive genetic, non-genetic litter, and residual variances and covariance components. The sire component will in fact estimate the strictly additive genetic variance plus a contribution, assumed negligible, made up of a small fraction of the interaction between loci involving additive effects (e.g. Kempthorne, 1955). Another assumption is that the effect of farm environment on pigs coming from different farms is negligible. If this is not the case, use of the sire component will lead to an overestimate of heritability, and this reservation has to be borne in mind.

A litter component of variation is made up of environmental influences common to the litter as a whole, but as estimated will also contain some non-additive genetic effects, principally those due to dominance (Kempthorne, 1955).

Approximate standard errors were calculated for the portions of the variance due to genetic effects and to litter effects (Woolf, 1960, personal communication) and standard errors of the genetic correlations by the method of Tallis (1959).

The pattern of correlations obtained for both genetical and residual (environmental) effects were examined by principal component analysis (cf. Kendall, 1957). The latent roots and vectors required were obtained with a standard computer programme.

Complete records were available for each pig on the following 35 measures and scores. For the location of some measures see Figure 1.

Κ

Daily gain on test-the average daily weight increment over the test period.

Food conversion (live-weight)—the total food eaten on test/total liveweight gain.

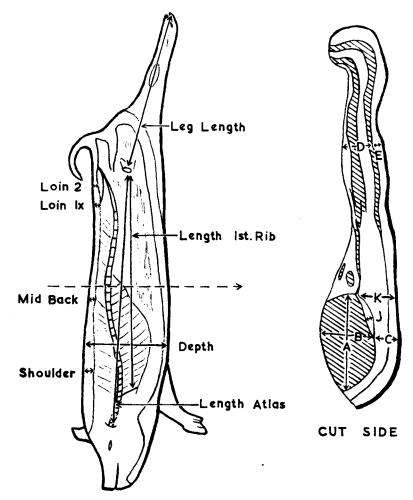


FIG. 1. Pig carcass showing the location of the carcass measurements.

- Food conversion (dead weight)—the total food eaten on test/total dead weight gain, the latter taken as carcass weight minus an estimated initial carcass weight of 30 lb.
- Last live-weight.
- Dressing out %-the carcass weight as % of last live-weight.
- Length to 1st rib—taken on the warm suspended carcass, from the *symphysis pubis* to the anterior edge of the first rib.
- Length to atlas—taken on the cold horizontal carcass from the symphysis pubis to the atlas joint.
- Vertebra number-lumbar plus thoracic.

Carcass depth-maximum depth from the sternum to the back.

- Leg length—from the tip of the toe to the anterior edge of the symphysis pubis.
- Loin length—from the anterior edge of the symphysis pubis to the posterior edge of the last rib.

Backfat thickness, measures of fat depth, taken along the mid line of the back (including skin thickness).

Shoulder-maximum depth at shoulder.

Mid-back—minimum depth in the middle of the back.

Loin 2-depth over middle of the rump muscle, the gluteus medius.

Loin 1x-maximum depth just anterior to the rump muscle.

Measures taken on the exposed face of the side when cut perpendicular to the line of the back at the posterior edge of the head of the last rib, exposing the 'eye' muscle or *longissimus dorsi*.

Eye muscle A-maximum width of eye muscle.

Eye muscle B-maximum depth of eye muscle perpendicular to A.

Fat depth C-fat depth over B.

Fat depth J-maximum depth of third layer of fat.

Fat depth K—fat depth over the latero-dorsal corner of the eye muscle. Eye muscle area—a planimeter area measure of a tracing of the eye muscle.

Streak E-fat depth of belly.

Streak D-depth of muscle and interspersed fat over E.

Carcass scores, assessed on a scale of 0-50 with intervals of 5, indicating the suitability of the carcass for bacon.

On the uncut side—shoulder score, ham score and carcass conformation score.

On the cut side-back rasher score and streak score.

Head weight--weight of head removed by a horizontal cut through the atlas joint.

Fillet weight-weight of psoas major.

Flare weight-weight of warm flare fat.

Food eaten per day at three weights during test.

I.-at 50 lb. live-weight.

II.—at 125 lb. live-weight.

III.—at 200 lb. live-weight.

Disease symptoms at any time on test (absent 0, present 1).

1.—scouring symptoms.

2.—'thumping' (symptom of lung disease).

RESULTS

The means of the 35 measures and scores for each sex and their overall standard deviations, corrected for differences between stations, seasons, and in last live-weight, are given in Table 1. In general, the gilts were the better bacon pigs, being more efficient, not so fat and with higher muscling and carcass scores. The gilts were also slightly less variable than the hogs. Body measures such as carcass length had low coefficients of variation (2-4%), growth, efficiency and food eaten had coefficients around 6-10%, measures of fat depth and muscle depth from 10-20%, while the various carcass scores had coefficients of variation from 15-30%.

The total variation was partitioned into additive genetic variance, nongenetic litter variance and residual variance. Approximate standard errors were attached to these portions. There was good agreement between the sexes in the various estimates; only one trait showed a significant difference between sexes for the additive genetic variance, and three traits for the litter

TABLE 1

Means of 35 traits, and their overall standard deviations after correction for differences in stations, seasons and slaughter weight

	Hogs		Gilts	
	Mean	S.D.	Mean	S.D.
Daily gain (lb./day)	1.52	0.14	1.51	0.12
Food con. (live-wt.) (lb. food/lb. gain)	3.41	0.24	3.31	0.23
Food con. (dead wt.) (lb. food/lb. carc. gain)	4.37	0.29	4·22	0.28
Dressing out %	73.5	1.69	73.9	1.62
Food I. (lb. food/day)	2.35	0.26	2.37	0.26
Food II (lb. food/day)	6.52	0.42	6.24	0 ∙46
Food III (lb. food/day)	7.59	0.50	7.23	0.53
Length to 1st rib (mm.)	802.2	19.6	809.7	20.0
Length to atlas (mm.)	931.3	22.5	938.1	23.6
Vertebra number	21.4	0.55	21.4	0.54
Carcass depth (mm.)	323.5	8.9	324.2	9.5
Leg length (mm.)	604.3	15.1	605.3	15.2
Loin length (mm.)	363.9	15.9	369.4	16.9
Head weight (lb.)	194-1 12.11	11.9- 0.74	<u>-196-5</u> 12.28	11-2 0·70
Backfat shoulder (mm.)	46.9	4.61	44·1	4·28
Backfat mid-back (mm.)	21.8	3.62	18.6	3.02
Backfat loin 2 (mm.)	28 ·1	4.60	23.8	4·23
Backfat loin 1x (mm.)	33.3	4·24	30.1	4·05
Fat depth C (mm.)	23.1	4·41	18.1	3.42
Fat depth J (mm.)	6.47	2.44	3.89	2.16
Fat depth K (mm.)	30.1	5·01	23.5	4·14
Streak E (mm.)	8.96	1.97	7.88	1.71
Flare weight (lb.) *	43 6 2 73	9-5 0.59	38-8 2-43	-8-6 0.54
Eye muscle A (mm.)	74·1	4.66	78·9	4·90
Eye muscle B (mm.)	44.8	4.54	48 ∙6	4.34
Eye muscle area (sq. cm.)	24.69	3.13	28.09	3.16
Streak D (mm.)	22.5	3.02	21.9	2.96
Fillet weight (lb.)*	17-8 · 1	19 0.12		19 0.12
Shoulder score (points)	24.5	9.16	24·2	9·24
Ham score (points)	25.6	7.17	28.8	6.93
Back rasher score (points)	23.9	10.50	38.9	7.75
Streak score (points)	31.9	5.81	31.9	5.37
Carcass conformation score (points)	21.8	8.98	23.6	9.13
Disease 1	0.25	0.61	0·19	0.55
Disease 2	0.14	0.50 Lillete	0.16	0 ∙51

Sum \mathcal{F}_{b} from Flash & sum \mathcal{F}_{b} two fillets. differences. Since at this level of probability (P = 0.05) as many differences as these are expected by chance alone, they can be dismissed and the estimates for each sex pooled. The pooled estimates are presented in Table 2 together with their approximate standard errors. The additive genetic portion was significant in all but one trait and contributed from 0.14 to 0.78 of the total variation in different traits. The litter variance contributed considerably less (0-0.28) of the total variation and was significant for only 11 traits. Of these, five were associated with gain and

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food eaten on test, suggesting that common litter environment had some influence on traits measured during life, but had little carry-over effect into carcass traits.

TABLE 2

Proportions of the variance attributed to different causes and their approximate standard errors

	Additive genetic variance (heritability)	S.E.	Litter variance	S.E.	Residual variance
Daily gain	0.41	0.099	0.15	0.053	0.44
Food conversion (live-wt.)	0.20	0.098	0.14	0.051	0.36
Food conversion (dead wt.)	0.58	0.101	0.14	0.051	0.28
Dressing out %	0.40	0.091	0.09	0.049	0.51
Food I	0.26	0.090	0.18	0.051	0.56
Food II	0.66	0.099	0.07	0.020	0.27
Food III	0.34	0.100	0.28	0.054	0.38
Length to 1st rib	0.60	0.101	0.12	0.021	0.28
Length to atlas	0.78	0.102	0.04	0.049	0.18
Vertebra number	0.35	0.093	0.07	0.020	0.58
Carcass depth	0.34	0.087	0.08	0.049	0.58
Leg length	0.20	0.094	0.08	0.020	0.42
Loin length	0 ·46	0.093	0.08	0.049	0 ·46
Head weight	0.49	0.096	0.10	0.020	0.41
Backfat shoulder	0.62	0.101	0.09	0.020	0.29
Backfat mid-back	0.73	0.097	0.004	0.047	0.27
Backfat loin 2	0.71	0.100	0.02	0.049	0.24
Backfat loin 1x	0.68	0.097	0.01	0·0 48	0.31
Fat depth C	0.65	0.096	0.02	0.048	0.33
Fat depth J	0.64	0.093	0 ∙00†	0.046	0.36
Fat depth K	0.73	0.099	0.004	0.048	0.27
Streak E	0.29	0.089	0.15	0.021	0 ·56
Flare weight	0.61	0.094	0.00	0.048	0.39
Eye muscle A	0 ·46	0.091	0.02	0 ·049	0·49
Eye muscle B	0.48	0.091	0.04	0.048	0 ·48
Eye muscle area	0.35	0.088	0.07	0.020	0 ∙58
Streak D	0.24	0.082	0.11	0·049	0 ∙65
Fillet weight	0.31	0.088	0.11	0.021	0 ∙58
Shoulder score	0.25	0.083	0.08	0.049	0.67
Ham score	0.35	0.090	0.11	0.021	0.54
Back rasher score	0.59	0.097	0.06	0.049	0.35
Streak score	0.32	0·0 86	0.08	0.049	0.60
Carcass conformation score	0.31	0.086	0.09	0.020	0.60
Disease 1	0.25	0.084	0.09	0.046	0.66
Disease 2	0.14	0.109	0.11	0.062	0.75

[†] Negative components—none significant.

The 35 traits fell into several broad categories measuring fat depth and fatness, muscling, body dimensions and so on, and it is convenient to consider these groups rather than the individual traits. Looking at the additive genetic portion of the total variation, that is the heritability, a general description is possible. The estimates of heritability of measures of fat depth ranged from 0.6 to 0.8, of muscling measures from 0.3 to 0.5, of carcass scores around 0.3 except for back-rasher score at 0.6, of body length from 0.5 to 0.8, and of measures of daily gain and food eaten on test from 0.3 to 0.6. The ranking of these categories and their general levels of heritability agree fairly well with other published results.

The phenotypic correlations, estimated from the total variances and covariances were very similar in the two sexes and their average is given in Table 3, each correlation having a standard error of about 0.02. The *genetic* correlations were estimated from the sire components of variance and covariance and have larger sampling errors. A number of specimen standard errors were calculated following Tallis (1959); these were all about 0.2. The agreement between the two sexes for these genetic correlations is therefore not expected to be as close as for the phenotypic correlations. Over the table as a whole the two sexes showed a similar pattern of correlations, although many differences were significant. Only analysis of further data can show whether these differences are real. The genetic correlations for the two sexes combined are given in Table 3. The phenotypic and genetic correlations behave similarly. The genetic correlations are, with few exceptions, of the same sign and of a higher absolute value than the phenotypic correlations.

It is hard to summarise these 1056 correlations in other than general It is the biological meaning of the correlation coefficients, the terms. implications of the degree and sign of relationship, which matters rather than the statistical significance. The first impression from the table is of high phenotypic and genetic correlations among traits concerned with one particular aspect of the pig. Measures of fat depth at several locations on the carcass are highly correlated, and so too are measures of food efficiency, measures of length, certain scores, appetite and to a lesser extent measures of muscling. One trait in each of these groups is probably sufficient to represent the whole group. The phenotypic and genetic correlations between traits of different categories are of a lower order and frequently not significant. There is a general high negative relationship of fat depth with measures of muscling and with carcass scores which are positively intercorrelated. The measures of length tend to be positively correlated with measures of muscling and some carcass scores but negatively correlated with fat depth, and the reverse holds for carcass depth. Daily gain and food conversion show quite a high negative correlation with each other, but differ in their associations with other groups of traits, in particular with muscle measures and daily food intake. Food conversion and daily food intake tend to be correlated positively with fat depth and negatively with measures of muscling and carcass scores. Among all 33 traits, head weight seems to be least dependent on the others.

Principal component analysis

This technique attempts to summarise all the correlations between a number of variates by expressing them in terms of a lesser number of new variates, called components, which are linear functions of the original variates. (These 'components' should be carefully distinguished from the 'components of variance' arising in the analysis of variance.) The first component is chosen so as to account for as much of the correlation pattern as possible. The second component is chosen to be uncorrelated with the first and to account for as much of the residual correlation pattern as possible, and similarly for successive components. It will usually take as many

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Head weight		<u> </u>		6655÷56	8,9,9,9
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Leg length			256668886995	÷÷÷÷ •10 •10	÷÷÷; •††
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	Daily gain Food con. (live wt.) Food con. (dead wt.) Dressing out % Food II Food II	Length to 1st rib Length to atlas Vertebra number Carcass depth Leg length Loin length Head weight	Backfat shoulder Backfat loin 2 Backfat loin 2 Backfat loin 1 x Fat depth C Fat depth K Streak E Fare weight	Eye muscle A Eye muscle B Eye muscle area Streak D Fillet weight	Shoulder score Ham score Back rasher score Straak score Carc. conform. score

TABLE 3

components as original variates to account for all the original correlation pattern. The objective is to represent the correlation pattern adequately by the first few components and to concentrate attention on these while neglecting the remainder. A measure of what part of the total pattern each component describes is given by its latent root, which is in fact the variance of that component.

The 'genetic' and 'environmental' correlations observed among 24 of the more important variates were chosen for principal component analysis.

TABLE 4

Vectors and latent roots of the first two principal components (I and II) of the genetic and environmental correlation matrices

		Genet	Genetic matrix		onmental atrix
		I	п	I	п
1.	Daily gain	0.03	0.24	0.09	0.28
2.	Food conversion (dead wt.)	0.11	0.16	0.22	-0.11
3.	Dressing out %	0.06	-0·19	0.14	-0·29
4.	Length to 1st rib	-0.18	0.29	0.08	0.24
-5.	Carcass depth	0.18	-0.38	0.00	-0·40
6.	Leg length	-0.18	0.03	-0.19	-0·21
7.	Backfat shoulder	0.30	0.04	0.05	-0·05
8.	Backfat mid-back	0.28	0.10	0.23	-0.06
9.	Backfat loin 2	0.29	0.05	0.32	0.14
10.	Backfat loin 1x	0.30	0.09	0.29	0.07
11.	Fat depth C	0.30	0.14	0.39	-0.01
12.	Fat depth J	0.25	0.14	0.22	-0.04
13.	Fat depth K	0.30	0.08	0.35	0.05
14.	Streak E	0.11	0.07	0.32	-0.11
15.	Flare weight	0.19	0.04	0.20	-0.14
16.	Eye muscle A	-0·22	-0·25	-0.09	-0.13
17.	Eye muscle B	-0.13	-0.19	-0.02	-0.04
18.	Streak D	0.04	−0 ·30	0.13	-0.15
19.	Fillet weight	−0 ·07	0.09	−0·09	0.11
20.	Shoulder score	-0·21	0.34	0.06	0.43
21.	Ham score	-0.02	-0.21	0.10	0.16
22.	Back rasher score	0·31	-0.09	-0·28	-0.05
23.	Streak score	0.03	~ 0·37	0.20	-0·18
24.	Carcass conformation score	0.20	0.28	0.06	0.43
	Latent root	8.63	3.83	4.22	3.40

Correlations, rather than covariances, were used since the scales of measurement of the different variates are not comparable. While the sum of the latent roots of the 24 components is 24 in each case, the first two latent roots add up to 12.46 and 7.62 for the genetic and environmental correlation matrices respectively. The third and fourth latent roots add up to 4.86and 4.00 for the two matrices respectively, and the other roots are comparatively unimportant. The first two components here give a reasonable approximation to the correlation pattern. Attention can be concentrated on these two components, so simplifying the problem of assimilating a mass of correlation coefficients.

In the matrix of genetic correlations 6 of the 24 latent roots turned out

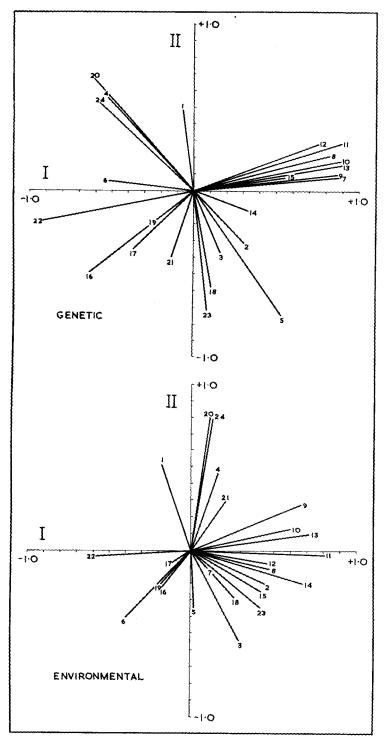


FIG. 2. Diagram of the vectors of the first two components (I and II) of the genetic and environmental correlation matrices. (Numbers on vectors refer to traits listed in Table 4.)

to be negative. This would be impossible in an ordinary correlation matrix, but in a derived matrix could be due to a variety of causes, e.g. sampling errors in the components of variance and covariance, or a failure of the assumptions made in the interpretation of these components. The principal components analysis may have the virtue of extracting two reliable variates from a mass of correlation coefficients which individually are of doubtful reliability.

The first two latent roots and their vectors for the genetic and environmental correlation matrices are given in Table 4. The vector coefficients for the genetic and environmental cases are seen to be in good agreement for the first two principal components. This means that the major genetic and major environmental relations between the traits considered are similar. The first principal component of the genetic correlation matrix has high positive vector coefficients for measures of fat depth and high negative vector coefficients for back rasher score, shoulder score, carcass conformation score, length and eye muscle depth and width. The first component could therefore be interpreted as some function of fatness which is negatively associated with measures of carcass desirability, muscle measures and length. The second principal component has high positive vector coefficients for length, carcass conformation score, shoulder score and daily gain and high negative vector coefficients for carcass depth, streak D and streak score, ham score, eye muscle width and % dressed carcass. Thus it appears to be associated with carcass dimensions, that is length and depth, and reflects greater muscle measurements both in the eye muscle and streak.

A visual representation of the first two principal components helps to summarise the information which the analysis provides about the correlation matrix. In the figure (Figure 2) the vector of the first two components of the genetic and environmental correlation matrices have been plotted and the points joined to the origin. To reflect the relative importance of the two components in explaining the correlation pattern, the vectors have been multiplied by the square root of the latent root and plotted on a common scale. Traits whose lines are close together will be similar in nature, those with lines at right angles to each other will be independent, and those with lines diametrically opposed are equivalent in that they measure the same quantity but differ in sign. It must be emphasised again that the first two vectors merely approximate the actual correlations which are set out in Table 3, so that the spatial arrangement in the figure accounts for only some part of the relations among traits.

In the genetic analysis the 8 measurements of fat depth (Nos. 12, 11, 8, 10, 13, 15, 9 and 7) are compactly grouped, showing that these measurements are measuring very much the same thing and in addition that back rasher score (No. 22) can be regarded as essentially a negative measure of fat depth. Eye muscle width (No. 16) and eye muscle depth (No. 17) and fillet weight (No. 19) lie together and are negatively associated with fat depth. Shoulder score (No. 20) and carcass conformation score (No. 24) are, apparently, largely determined by the length of the carcass (No. 4) and are opposite to carcass depth (No. 5). Streak score (No. 23) is close to the measurement of muscle in streak D (No. 18) and removed from the measure of streak fat (streak E, No. 14) which shows a closer affinity to other fat measurements. The expected relationships between daily gain (No. 1), food conversion (dead weight) (No. 2) and dressing out % (No. 3) can be seen although

the short radii shown on this figure indicates that the correlations explained by these first two principal components are not high.

The figure of components for the environmental correlation matrix is broadly similar to the genetic one but individual traits are more dispersed and do not show the same close associations. There also appears to have been a rotation of the axis of the diagram, but without any fundamental change in relationships.

DISCUSSION

The practical significance of the estimated genetic parameters lies in the prediction of improvement through selection. The expected genetic change in a population through selection is determined by the heritability of each trait, the selection differential applied and the genetic correlation among the characters under study.

The traits most commonly investigated in pigs have been daily gain, food conversion, backfat thickness and carcass length. A resumé of the estimates of the heritabilities for these traits calculated from progeny testing station records is given in Table 5.

TABLE 5

A summary of the heritabilities of four traits estimated from progeny testing station records

	Group feeding				Individual feeding			
	1	2	3	4	5	6	7	8
Daily gain	0.24		0.25	0.21	0 ·15	0.50	0.44	0 ·41
Food conversion		0.30	0.18	·	—	0 ∙58	0 ∙44	0.20
Carcass length	0.47	0.40	0.61	0.66	0.39	0.48	0.45	0.60
Backfat thickness	0.54	0.43	0.54	0·48	0 ·43	0.55	0 ∙47	0.66

- (1) Lush (1936). Danish Landrace, 83 sires.
- (2) Fredeen (1953). Canadian Yorkshire, 644 sires.

(3) Johansson and Korkman (1950). Swedish Landrace, 1693 sires.

(4) Osterhoff (1956). Swedish Landrace, 640 sires.

(5) Broderick (1960). Irish Large White, 60 sires.

(6) Fredeen and Jonsson (1957). Danish Landrace, 468 sires.

(7) Jonsson and King (1962). Danish Landrace, 935 sires.

(8) Smith, King and Gilbert (here). British Large White, 200 sires.

There is no basic necessity for the estimates of heritability relating to various populations and environments to agree. In view of the sampling errors and the various biases to which they are liable, there is good agreement in the estimates of heritability of backfat thickness and carcass length among the different authors, and good agreement within feeding regime for daily gain and food conversion. The different degree of heritability, however, for these two latter traits in the two sexes found by Fredeen and Jonsson (1957) was not apparent here. Jonsson (1959) compared the variation among group-fed and individually-fed pigs and found that the higher estimates of heritability of daily gain in the latter arose largely from the reduction of the intra-test-group (intra-litter) component, and ascribed this reduction to the elimination of intra-litter competition when pigs are individually fed. In agreement with the estimates of Fredeen (1953) and Jonsson and King (1962) heritabilities of visual scores of carcass suitability such as ham score, shoulder score and carcass scores tended to be less than the heritabilities of measurements of carcass desirability especially fat depth and carcass length. Few estimates of the heritability of eye muscle measurements appear in the literature. An estimate of 0.66 for eye muscle area reported by Fredeen (1953) and one of 0.29 for eye muscle depth by King (1957) may be compared respectively with the estimates 0.35 and 0.48 reported here.

Analyses of testing station records have been a common means of investigating the genetic parameters of pig populations but this type of data may be somewhat artificial. Pigs entering a testing station are usually of selected parents, of a uniform weight and conform to the ideals of the breeder. The progeny of a sire experience the same pre-test farm environment, the effect of which may not be insignificant (Lauprecht and Walter, 1960; Broderick, 1960; Jonsson and King, 1962), and tend to be contemporary at the station. Breeders may favour different ideals or some may be more successful than others so that dissimilar strains exist. On the other hand only those breeders with a common goal may enter into progeny testing. These factors, if they are relevant, may affect the estimates of heritability in testing station data and should be borne in mind in interpreting and applying the estimates of genetic parameters in practice.

The selection differential for any one trait will be determined by the emphasis it receives when breeders make their selections, and by the choice available among breeding animals. Of the breeders who progeny-tested Large White boars in Britain in 1960 only 25% tested more than one boar per year so that within herds the choice among boars tested at the stations is very limited. On the other hand the individual breeder may choose from the total of 141 boars tested. A strong demand for progeny of high-ranking boars indicates that this type of selection is common. The selection differential depends not only on the intensity of selection but also on the observed variability of the trait. That different degrees of variability may exist in different pig populations is brought out by comparing Danish Landrace (Jonsson and King, 1962) and British Large White pigs all fed individually at testing stations. The standard deviations, averaged over the two sexes, for four traits are given below.

	British Large White (1)	Danish Landrace (2)
Daily gain (lb./day)	0.13	0.07
Live food conversion (lb. food/lb. gain)	0.23	0.14
Length to atlas (mm.)	23.0	20.0
Backfat thickness (mm.)	3.38	2.94

(1) Smith, King and Gilbert (here).

(2) Jonsson and King (1962).

British Large Whites are about twice as variable as Danish Landrace for daily gain and food conversion and are also more variable for backfat thickness and carcass length, though the latter two are not quite identical measurements in the two populations. Because of this higher degree of variability with effectively the same heritabilities, a greater rate of improvement should be possible (with the same intensity of selection) in British than in Danish pigs. Referring back to the work of Jonsson (1959) in comparing the variation and heritability of individually- and group-fed pigs the higher heritability of daily gain noted in the former must be set against the concurrent reduction in variation. Because the selection differential, with the same intensity of selection, will be less, the genetic improvement on individual feeding may not be greatly increased in spite of the higher heritability. It is interesting to speculate on why different levels of variability exist in the Danish Landrace and British Large White. The lower variability of the Danish Landrace may be due to the effects of long term selection in improving these traits as illustrated by Clausen and Nørtoft Thomsen (1961) for backfat thickness. The difference may also be partly due to the different feeding systems employed.

By selection for one or several traits the breeder indirectly exerts selection pressure on other traits. The value of his selections may be nullified if

TABLE 6

Expected response from one generation of selection for various traits when the best 25% of boars tested are used

Selection for improvement in	Daily gain (lb./day)	Food conversion (dead wt.) (lb. food/ lb. carcass	Average backfat (mm.)	Length (mm.)	Eye muscle area (cm²)	Carcass confor- mation (points)
Daily gain	0.039	-0.06	-0·05	1.4	0.34	0.8
Food conversion (dead wt.)	0.025	-0.12	−0 ·41	1.5	0.33	1.4
Average backfat	0.001	-0.03	1.84	3.3	0.46	1.5
Length	0.007	-0.02	0.68	7.9	0.08	1.7
Eye muscle area	-0.014	-0.04	-0.72	0.6	0.88	0.5
Carcass conformation	0.012	0.02	0.80	4.5	0 ·16	2.3

traits are incompatible but increased if desirable traits have favourable genetic correlations. The genetic correlations presented in Table 3 provide information about the expected correlated response in one trait when selecting for another. To bring out the nature and sizes of the correlated responses those expected in six characters following selection for any one of them are shown in Table 6, when for example the best 25% of tested boars are used for breeding. These six characters were chosen as of primary importance by the National Pig Progeny Testing Board.

Favourable responses are negative for food conversion and backfat thickness and positive for the other traits. Apart from that between daily gain and eye muscle area the correlated responses in the above table are favourable. However, they provide only some part of the response obtainable by direct selection for each trait. The compatibility of improvements in speed of growth and food conversion with reduction in backfat thickness and improvement in carcass desirability makes the improvement on these two fronts an apparently straightforward process. From the overall efficiency of pig production their compatibility with a third front, that of reproductive performance, is very relevant but has still to be investigated.

Comparisons of the genetic correlations, used in Table 6 and given extensively in Table 3, with other published estimates are not easy because of the high sampling error of all estimates. As far as can be judged, there is substantial agreement with the various estimates presented by Johansson and Korkman (1950), Jonsson (1959) and Jonsson and King (1962). There has been no confirmation either here or in the literature of an important antagonism between food conversion and carcass leanness reported by Dickerson (1947) in inbred lines of Poland China pigs. There would appear to be a progressive reduction in the genetic correlation between daily gain and food conversion from about -0.9, down to -0.6, as one moves away from the more restricted system of Danish feeding towards complete *ad lib*. feeding.

The results obtained from the principal component analysis have been described in some detail and it only remains to discuss their wider implica-The two analyses carried out on the environmental and genetical tions. components respectively show that in the latter much more of the observed variation in the correlation matrix can be explained by two principal com-This is to be expected as the genetical correlation matrix has ponents. excluded many of the attenuating effects produced by errors of measurement. The analysis to this extent makes a closer approach to the underlying relationships but leaves a major problem unsolved. This is to know if, and in what manner, principal components revealed by statistical analysis can be related to biological mechanisms. While it is true that a biological mechanism can give rise to an identifiable component, the reverse is by no means necessarily true. Thus although it is tempting to identify the first principal component with some function of fatness, and advocates of factor analysis would undoubtedly do so, this step may not be justified. there are physiological measures of fat metabolism available with which to correlate the fatness factor the identification of factors would be misleading, particularly since they are so dependent on the spectrum of measurements chosen for analysis.

SUMMARY

Estimates of heritabilities and genetic correlations among 35 measurements and scores of British Large White bacon pigs are reported. The data came from pigs tested at the five National Progeny Testing Stations during the period autumn 1957 to spring 1959, and comprised full records on 1936 pigs from 200 sires. Independent analyses were carried out for each sex, and adjustments were made to the data for differences among stations, six-monthly periods and weight at slaughter.

Genetic parameters were estimated from sire components of variation and covariation obtained by conventional heirarchical analyses of variance and covariance. Estimates of the heritabilities and their standard errors are given in Table 2, and of genetic and phenotypic correlations in Table 3. These estimates, which agree in general with other estimates in the literature, indicate that a large part of the variation and covariation is of genetic origin and that carcass traits, growth rate and food conversion efficiency are amenable to change by selection. Moreover, no serious antagonisms were found to exist with regard to improvement by selection.

An attempt has been made to summarise the correlation matrix pattern among 24 of the more important traits by using a principal component analysis. The first two principal components account for a disproportionate fraction of the correlation pattern especially of the genetic correlation matrix. Two principal components are given for each trait; the first may be associated with measurements of fat depth.

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