GENERAL, GROUP AND SPECIAL SIZE FACTORS

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INTRODUCTION

The question as to how far growth factors act generally and how far locally is of interest both in relation to problems of evolution and in connection with the physiology of gene action. Widely different views continue to be expressed. CASTLE (1914, 1922, 1923, 1924a, 1924b, 1929) has maintained that differences in size within a species are due practically wholly to general factors. He recognizes the existence of genes which act locally such as those which determine short ears in mice and in sheep, but considers such genes as of negligible importance in determining general size. He also recognizes that body form is to some extent a function of size, holding that factors which are general in action need not determine the same rate of growth in all parts, that is, that there are growth relations of the sort which HUXLEY terms heterogonic. CASTLE (1922) has supported this viewpoint by demonstration of high correlations between measurements from rabbit populations including the F_2 from a cross between strains of which one was more than two and a half times as heavy as the other.

CASTLE's first statement (1914) was based on the high correlations in a series of measurements of rabbit bones made by MACDOWELL. A few years later (1918), I attempted an analysis of the same data by a special method which it is the purpose of the present paper to develop. It may be noted here that this analysis confirmed CASTLE's interpretation to the extent that factors for general size were indicated to be much the most important in determining the size of each part (and *a fortiore* of general size) but also indicated the existence of factors (not necessarily genetic) with various degrees of localization of effect.
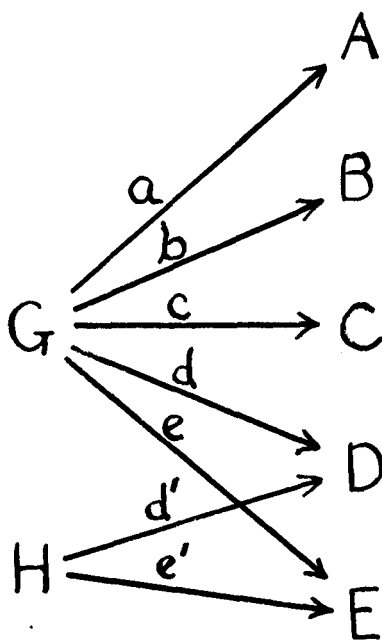
DAVENPORT (1917) from a study of human data reached conclusions considerably at variance with those of CASTLE: "The conclusion that follows from a consideration of these data is that general factors control growth to a degree that may be estimated at less than half. On the other hand, special factors are present that control independently the growth of the various elements that go to make up stature." SUMNER (1923, 1924) found a somewhat similar situation on analyzing data from large local collections of subspecies of *Peromyscus maniculatus*. A more extreme mosaic viewpoint with respect to growth was expressed by MJOEN (1923) who concluded that crosses between strains (rabbits, men) differing in size were likely to yield serious disharmonies in F_2, as a consequence of independent segregation of locally acting growth factors.

It is agreed by most authors that the results of crosses between ordinary strains of different size give evidence of Mendelian heredity but require the assumption of multiple factors. CASTLE (1929) has been inclined recently to question the applicability of this scheme, on the basis of the absence of demonstrable linkage with color factors in a cross between varieties of rabbits of widely different size. GREEN (1931b), however, has presented evidence for such linkage in a cross between the common mouse (*Mus musculus*) and the small related species (*Mus bactrianus*) in which the former introduced 3 recessive factors, represented by dominants in the latter. The same data gave evidence for important group (as opposed to general) factors in that one of the recessive color factors (brown) showed linkage with large size of the leg bones and body length, but not with head and tail measurements, while another showed such linkage only with body and tail lengths. CASTLE and GREGORY (1929, 1931) have given data on the mode of action of the general factors which distinguish large and small strains of rabbits. They find that while these breeds produce eggs of the same size, a difference in the rate of growth and division is recognizable as early as the 8 to 16 cell stage and continues from that time without affecting the rate of differentiation.

<center>METHOD OF ANALYSIS</center>

As there is general agreement on at least the existence of growth factors with various modes of action, it would seem that further progress must depend on quantitative evaluations of their relative importance in representative cases. As noted above, I attempted a number of years ago (1918) to make such an evaluation of a system of correlation coefficients relating to rabbit bones, using data published by CASTLE. The method followed was that of path coefficients. The results were expressed in terms of the

portion of the squared standard deviation of each measurement, due to each kind of factor: general, group or special. (In this analysis, factor is not to be understood as synonymous with gene. By the general factor is meant the entire array of factors, environmental as well as genetic, which have a general effect on growth. The group factors and special factors are to be interpreted similarly. The question of the apportionment of these into genetic and environmental components is discussed later.) The method did not yield a unique result, but merely certain limits and the final figures were obtained by a somewhat unsatisfactory process of averaging. The purpose of the present paper is to show the application of a slight modifica-

tion of this approach. The method of least squares is used to determine a system of path coefficients relating each measurement to a single general factor in such a way that the observed correlations will be accounted for with the least possible residual. These residuals if of significance are then used in estimating the degree of determination of each measurement by group factors.

Let A,B,C,D, and E stand for the different parts of the animal for which series of measurements are available. The path coefficients measuring the variability due in each case to the general factor G (in terms of the standard deviation of the dependent variable) are represented by appropriate small letters, $a = p_{AG}$, $b = p_{BG}$, etc. As each variable is related to G along

only one indicated path, each path coefficient is identical in value with the correlation between the variable in question and the general factor. The correlation between any two of the variables is simply the product of the two path coefficients, measuring the relations of each to the general factor, in so far as it is determined by the latter. Thus if G is the only common factor in the growth of A and B, $r_{AB} = ab$. If on the other hand, there is some other common factor, contributing to the correlation between certain of the variables, as H is represented as doing in the case of D and E, there is an additional term in the correlation: $r_{DE} = de + d'e'$; where $d' = p_{DH}$, $e' = p_{EH}$. Our purpose is to find the values of the coefficients pertaining to G which will account as completely as possible for the observed correlation and thus will give the *maximum* estimate of determination by general factors and the *minimum* by group and special factors.

If there are n variables, $n(n-1)/2$ correlation coefficients can be calculated, giving this number of observation equations of the type, $ab = r_{AB}$. No solution is possible with only two variables (one equation). With three variables, yielding three equations, an exact solution is always formally possible, although if one of the unknowns comes out greater than unity, the interpretation as the correlation with the general factor becomes impossible. With more than three variables, the number of observation equations is greater than the number of unknown path coefficients. A solution without significant residuals, after fitting by least squares, is at least suggestive of complete dependence of the correlations on general factors, while the appearance of significant residuals demonstrates the existence of secondary group factors and indicates something of their nature.

For ready application of the method of least squares, the unknown quantities in the observation equations must be separated. One obvious method of doing this in the present case is by the use of logarithms, writing the observation equations

$$\log a + \log b = \log r_{AB}, \text{ etc.}$$

Unfortunately the logarithmic transformation expands differences between small correlations and contracts differences between larger ones and the application of the method of least squares would give an unduly good fit to the former at the expense of the latter. Actually, the large correlations have the smaller standard errors and should be given more weight in fitting. R. A. FISHER gives a transformation of the correlation coefficient with approximately uniform standard errors at all values but this does not give a separation of the unknowns. The method followed, capable doubtless of some improvement by proper weighing, has been to fit the untransformed correlations by the trial and error method. Assume that fairly good

first estimates can be made of the path coefficients, a_1 for a, b_1 for b, etc. and write $a = a_1 + \Delta a_1$, etc. The small errors, Δa_1, Δb_1, etc., are now the unknown quantities which are to be determined.

$$(a_1 + \Delta a_1)(b_1 + \Delta b_1) = r_{AB}$$
$$b_1 \Delta a_1 + a_1 \Delta b_1 = r_{AB} - a_1 b_1 \text{ approximately.}$$

The separation of Δa_1 and Δb_1 is accomplished by ignoring the product term $\Delta a_1 \Delta b_1$ which is of the second order of smallness. The solution will be slightly in error, but, on repetition of the process, the error should be reduced to negligible proportions.

A first estimate of the ratio $\dfrac{b_1}{a_1}$ can be obtained by averaging the ratios

$\dfrac{r_{BC}}{r_{AC}}, \dfrac{r_{BD}}{r_{AD}}, \dfrac{r_{BE}}{r_{AE}}$ since these equal $\dfrac{bc}{ac}, \dfrac{bd}{ad}$ and $\dfrac{be}{ae}$ respectively, if wholly de-

pendent on the general factor. The ratios $\dfrac{c_1}{a_1}, \dfrac{d_1}{a_1}$, etc. can be estimated sim-

ilarly. b_1, c_1, d_1, etc. having been expressed in terms of a_1, all of the observation equations can be expressed in terms of a_1^2. Addition of these equations yields a solution for a_1 and consequently for b_1, c_1, etc. The first corrections, Δa_1, Δb_1, etc., can now be found from the normal equations written in the usual way. The latter take a form yielding immediate solution for each of the other corrections in terms of Δa_1 which can then be determined by substitution in one of the equations.

ANALYSIS OF A RABBIT POPULATION

It will be desirable at this point to introduce actual data. We will use the same system of rabbit measurements analyzed in the previous paper. Table

TABLE 1

Statistics of 5 bone measurements in population of about 370 rabbits (F_1 of a cross of black and tan with Polish and backcross of F_1 to the Polish). Basic data of MacDowell *(1914), mean and standard deviation (SD) (both in mm) given by* Castle *(1914), C, coefficient of variation; p, path coefficient relating measurement to general factor; pC, percentage regression on general factor (in arbitrary units).*

	MEAN	SD	C	p	pC
L (length of skull)	73.0	3.6	4.93	.846	4.17
B (breadth of skull)	40.0	1.7	4.25	.775	3.30
H (humerus)	66.0	2.6	3.94	.897	3.53
F (femur)	82.8	3.1	3.74	.930	3.48
T (tibia)	96.0	3.4	3.54	.875	3.10

1 gives the mean, standard deviation (SD) and coefficient of variation (C) of the 5 rabbit bones as given by CASTLE. The next column (p) shows the least square determination of the path coefficients, relating these parts to the general factor, which will best account for the correlation coefficients. The latter are given in table 2 followed by the values estimated as due to

TABLE 2

Analysis of correlations (published by CASTLE *1914) between measurements of* MACDOWELL'S *rabbits (table 1): r, correlation coefficients; $p_{1G}p_{2G}$, contribution of maximized general factor to correlation (products of p's of table 1); Δ, differences of preceding, the squares of which are minimized; $r_{12\ G}$ partial correlations with maximized general factor; $p'_{1G}p'_{2G} = (0.945\ p_{1G}p_{2G})$; contribution of general factor, reduced to eliminate spurious negative contributions; Δ¹, revised differences; $r'_{12 \cdot G}$, revised partial correlations.*

	r	$p^1_G p_{2G}$	Δ	$r_{12 \cdot G}$	$p'_{1G}p'_{2G}$	Δ'	$r'_{12 \cdot G}$
L-B	0.750	0.656	+0.094	+0.28	0.626	+0.124	+0.34
L-H	0.743	0.759	−0.016	−0.07	0.724	+0.019	+0.07
L-F	0.760	0.787	−0.027	−0.14	0.751	+0.009	+0.04
L-T	0.701	0.740	−0.039	−0.15	0.706	−0.005	−0.02
B-H	0.675	0.695	−0.020	−0.07	0.663	+0.012	+0.04
B-F	0.674	0.721	−0.047	−0.20	0.688	−0.014	−0.05
B-T	0.658	0.678	−0.020	−0.07	0.647	+0.011	+0.03
H-F	0.857	0.834	+0.023	+0.14	0.796	+0.061	+0.30
H-T	0.791	0.785	+0.006	+0.03	0.749	+0.042	+0.17
F-T	0.858	0.815	+0.044	+0.25	0.777	+0.081	+0.38

the general factor (that is, the products of the path coefficients taken in the appropriate pairs). Evidently no single factor can account for the 10 correlations exactly. The differences, minimized by this method, are given in the next column. The correlation between length and breadth of skull shows the greatest excess (+.094) over that which can be due to the general factor. The correlations between the long bones show some excess although that between humerus and tibia is practically zero. The correlations between skull measures and leg measures are all in defect. The method of calculation is such that positive and negative differences must balance each other. We will return to the interpretation of these negative differences presently.

The significance of these differences can perhaps be appreciated best by calculating the partial correlations for constant general size. The formula in the case of $r_{LB \cdot G}$ is

$$r_{LB \cdot G} = \frac{r_{LB} - r_{LG}r_{BG}}{\sqrt{(1 - r^2_{LG})(1 - r^2_{BG})}} = \frac{r_{LB} - lb}{\sqrt{(1 - l^2)(1 - b^2)}}$$

of which the numerator is the difference just calculated. The values are given under the heading $r_{12 \cdot G}$.

The number of measurements was between 370 and 380, giving a standard error of 0.05 or less for ordinary partial correlation coefficients. The standard errors of coefficients based on minimized residuals should be smaller. With at least six of the ten partial correlations exceeding twice their standard errors, there can be no doubt of the reality of residual contributions to the primary correlations. The three positive correlations indicate group factors which seem reasonable enough and are quite in agreement with the earlier analysis. Clearly length and breadth of the skull vary together to some extent, independently of general size ($r_{LB \cdot G} = 0.28$). The same is true of the bones of the hind leg ($r_{FT \cdot G} = 0.25$) and probably of the proximal long bones of the fore and hind legs ($r_{HF \cdot G} = 0.14$).

The negative correlations require some interpretation. To some extent, excessive growth in one part may interfere with growth in other parts which would tend to create negative correlations with the latter. For the most part, however, the negative residual correlations are undoubtedly spurious from the physiological standpoint. They are merely a necessary consequence of the process of minimizing the residuals. The partial correlations are those which one would expect in a hypothetical population in which all rabbits were selected as identical in the general size index. The existence of any variability, independent of general size, would require that in these animals parts which happened to be above the average must necessarily be balanced by other parts below the average, merely by the act of selection. Putting it in another way, if there are both factors with a physiological effect on all parts and also ones acting on special parts, a population in which the former were constant would still vary in any chosen general size index because of the independent variability of the latter group. Thus the process of minimizing the squared residuals necessarily assigns too much to the general factor. The figures become more intelligible physiologically if the path coefficients are all proportionately reduced by the slight amount necessary to avoid significant negative residuals. The average of the four observed correlations between the head and the hind leg measures is 0.698 while the corresponding calculated values average 0.732. By multiplying all calculated values by the ratio $0.698/0.732 = 0.954$, equivalent to multiplying each of the five path coefficients by 0.977 ($= \sqrt{0.954}$) the spurious negative residuals are practically eliminated. The revised correlations due to the general factor, the revised residuals, and the revised partial correlations are shown in the last three columns of table 2. These probably give a fairer idea of the importance of group factors than

the preceding set. The residual of the correlation between length (L) and breadth (B) of skull indicates that common factors not affecting the legs contributed $+0.124$ to the total correlation between these skull measures. Letting l' and b' be the path coefficients relating L and B respectively to the indicated common head factor, $l'b' = 0.124$. The portion of the variance of L determined by this common factor is l'^2 and of B is b'^2. If these be assumed equal, they both equal $l'b'$, giving 12 percent as the estimate of the portion of the variance of each, determined by this factor. However, more of the variance of L is determined by the general factor than in the case of B, leaving less to be determined by other factors. It is, perhaps, better to assume that the same proportion of the residual variance is determined by the common head factor. An estimate of this proportion can be obtained by applying the partial correlation for constant general factor to the proportion of the variance left on subtracting that due to the general factor. In the case of L this gives 11 percent ($=0.34 \times 0.32$) as due to the head factor and in the case of B 15 percent (0.34×0.43). The two methods are identical if the variables are equally determined by the general factor.

	GENERAL	GROUP	GROUP	SPECIAL
Length of Skull (L)	68	11 (head)		21
Breadth of Skull (B)	57	15 (head)		28
Humerus (H)	77	4 (legs)	3 (proximal)	16
Femur (F)	83	3 (legs)	2 (proximal)	9
			3 (hind leg)	
Tibia (T)	73	5 (legs)	5 (hind leg)	17

These estimates differ somewhat from those reached in the previous paper, but the differences are largely formal. In that paper, the skull measures were given more weight and the leg measures less in the conception of general size. Thus some of the variability assigned here to the head group was assigned to the general factor, but this necessarily involved the assignment of more influence to the leg group and less to the general factor in the case of the legs. The conception of general size given by this method is of course a function of the variables selected. If a large number of head measures were used and little else, the former would have undue weight and *vice versa*. This relativity of the conception of general size must be borne in mind in interpreting all of the results.

HETEROGONIC GROWTH

It was stated that this method of estimating the importance of the general factor does not assume proportional growth of all parts as due to the latter. It is interesting to find the relation between change in each part and

change in the hypothetical general factor. The regression of each part on general size is proportional to the product of the coefficient of variation into the path coefficient. These products are given in table 1 under the head pC. It appears that with increasing size the breadth of the skull falls off relatively to the humerus and femur while the length of the skull becomes disproportionately great. The larger rabbits are more dolichocephalic than the smaller ones, as noted by CASTLE (1914).

At this point the question is likely to be raised as to whether it would not be well to get rid of the relativity of the conception of general size by treating the general factor as one causing proportionate growth in all parts. Under this conception, the products pC must all be alike and consequently the path coefficients must be proportional to the reciprocals of the coefficients of variation. This leaves only one unknown to be determined. One may equate the observed correlations each to a product of the type X^2/C_1C_2 and find that value of X^2 which will make the sums equal (thus minimizing the residuals), or, otherwise, that which will avoid significant negative residuals. Unfortunately, the residuals that result from this method are a meaningless lot as compared with those obtained by the other method. A positive residual may as before indicate a common factor apart from general size, but it may also indicate that the two parts otherwise unrelated happen to increase to a disproportionate extent with increase in general size. There seems to be no way of disentangling the effects of group factors from effects of heterogony with this method of attack.

ANALYSIS OF F_1 AND F_2 FROM A WIDE CROSS

The data analyzed above were not satisfactory for determining the roles of heredity and environment in relation to the various classes of growth factors—general, group and special. They consisted of a mixture of F_1's of a cross between two races of rabbit, differing considerably in size, with the backcross to the smaller race. It has therefore seemed of interest to apply the same sort of analysis separately to the F_1 and F_2 generations of a cross between races of rabbits (Polish and Flemish giant) at opposite extremes in size, using the figures published by CASTLE (1922). It seemed desirable to have each system of correlations depend on exactly the same individuals throughout. Accordingly only those rabbits were considered for which all 7 of the chosen measurements, body weight, length and breadth of skull (posterior zygoma), ear length and lengths of humerus, femur and tibia, were complete. There were 112 F_2's with complete records and the constants and correlations have all been recalculated to apply to just these animals. In making the calculations, their weights were grouped in 50 gram

intervals (1550–1599), the skull breadth in 0.5 mm intervals, the ear length
in 0.2 mm intervals and the others in 1.0 mm intervals. SHEPPARD'S cor-
rection was used in calculating the standard deviations for their own sake
and for use in calculating the correlation coefficients. There were only 27
F_1 rabbits available and the statistical constants were obtained without
grouping. The data and deductions are presented in tables 3 to 6 in a simi-

TABLE 3

Statistics of 27 rabbits of F_1 of cross between Polish and Flemish giant calculated from data of CASTLE
1922. Symbols as in table 1. Weight in grams. Other measure in mm.

	MEAN	SD	C	p	pC
W (weight)	2506.00	187.00	7.47	.338	2.52
L (length of skull)	75.55	1.31	1.74	.730	1.27
B (breadth of skull)	42.23	1.01	2.40	.421	1.01
E (ear length)	10.94	.38	3.44	.419	1.44
H (humerus)	66.18	1.18	1.78	.790	1.41
F (femur)	83.39	1.65	1.97	.824	1.47
T (tibia)	96.19	2.79	2.38	.596	1.42

TABLE 4

Analysis of correlations between measurements of the F_1 rabbits described in table 3. Symbols as in
table 2 except that column giving contribution of sex to correlations is introduced. This is not used in
calculating Δ, $r_{12 \cdot G}$, *etc.* $p'_{1G}p'_{2G}=0.749 \ p_{1G}p_{2G}$.

	r	P1GP2G	CONTRIBU-TION OF SEX	Δ	$r_{12 \cdot G}$	P$'_{1G}$P$'_{2G}$	Δ'	$r'_{12 \cdot G}$
W-L	0.408	0.247	+0.01	+0.161	+0.25	0.185	+0.223	+0.30
W-B	0.352	0.142	−0.12	+0.210	+0.25	0.106	+0.246	+0.28
W-E	0.176	0.142	+0.02	+0.034	+0.04	0.106	+0.070	+0.08
W-H	0.216	0.267	−0.03	−0.051	−0.09	0.200	+0.016	+0.02
W-F	0.172	0.279	−0.03	−0.107	−0.20	0.209	−0.037	−0.06
W-T	0.037	0.201	−0.04	−0.164	−0.22	0.150	−0.113	−0.14
L-B	0.388	0.307	+0.02	+0.081	+0.13	0.230	+0.158	+0.22
L-E	0.396	0.306	0.00	+0.090	+0.15	0.229	+0.167	+0.23
L-H	0.572	0.577	+0.01	−0.005	−0.01	0.432	+0.140	+0.25
L-F	0.504	0.602	0.00	−0.098	−0.25	0.451	+0.053	+0.10
L-T	0.351	0.435	+0.01	−0.084	−0.15	0.326	+0.025	+0.04
B-E	0.243	0.176	−0.05	+0.067	+0.08	0.132	+0.111	+0.13
B-H	0.323	0.333	+0.10	−0.010	−0.02	0.249	+0.074	+0.11
B-F	0.251	0.347	+0.07	−0.096	−0.19	0.260	−0.009	−0.02
B-T	0.118	0.251	+0.11	−0.133	−0.18	0.188	−0.070	−0.09
E-H	0.448	0.331	−0.01	+0.117	+0.21	0.248	+0.200	+0.29
E-F	0.206	0.345	−0.01	−0.139	−0.27	0.258	−0.052	−0.08
E-T	0.097	0.250	−0.02	−0.153	−0.21	0.187	−0.090	−0.11
H-F	0.653	0.651	+0.02	+0.002	+0.01	0.487	+0.166	+0.32
H-T	0.423	0.471	+0.03	−0.048	−0.10	0.353	+0.070	+0.11
F-T	0.840	0.491	+0.02	+0.349	+0.77	0.368	+0.472	+0.79

lar form to that used in the preceding case. The figures differ but slightly from those given by CASTLE (in so far as presented by him). Comparison of the coefficients of variation of the two populations brings out the uniformly greater values in F_2 which CASTLE discussed as evidence for genetic segregation of multiple factors.

TABLE 5

Statistics of 112 rabbits of F_2 of cross between Polish and Flemish Giant, calculated from data of CASTLE (1922). Symbols as in table 1.

	MEAN	SD	C	p	pC
W (weight)	2127.0	255.00	11.99	0.784	9.40
L (skull length)	73.5	3.09	4.21	0.849	3.57
B (skull breadth)	40.9	1.17	2.86	0.514	1.47
E (ear length)	10.7	0.59	5.47	0.704	3.85
H (humerus)	64.1	2.93	4.57	0.934	4.27
F (femur)	80.5	3.80	4.72	0.929	4.38
T (tibia)	93.5	4.82	5.15	0.852	4.39

TABLE 6

Analysis of correlations between measurements of F_2 rabbits described in table 5. Symbols as table 2, $p'_{1G}p'_{2G}=0.900\ p_{1G}p_{2G}.$

	r	P1GP2G	CONTRIBUTION OF SEX	Δ	$r_{12}\cdot G$	P'1GP'2G	Δ'	$r'_{12}\cdot G$
W-L	0.731	0.666	0.00	+0.065	+0.20	0.600	+0.131	+0.33
W-B	0.495	0.403	−0.06	+0.092	+0.17	0.363	+0.132	+0.23
W-E	0.594	0.552	0.00	+0.042	+0.10	0.497	+0.097	+0.20
W-H	0.717	0.732	0.00	−0.015	−0.07	0.659	+0.058	+0.19
W-F	0.676	0.728	−0.03	−0.052	−0.23	0.655	+0.021	+0.07
W-T	0.583	0.668	−0.04	−0.085	−0.26	0.601	−0.018	−0.05
L-B	0.491	0.436	0.00	+0.055	+0.12	0.393	+0.098	+0.19
L-E	0.663	0.598	0.00	+0.065	+0.17	0.538	+0.125	+0.28
L-H	0.743	0.793	0.00	−0.050	−0.26	0.714	+0.029	+0.11
L-F	0.744	0.789	0.00	−0.045	−0.23	0.710	−0.034	+0.12
L-T	0.679	0.723	0.00	−0.044	−0.16	0.651	+0.028	+0.08
B-E	0.442	0.362	0.00	+0.080	+0.13	0.326	+0.116	+0.18
B-H	0.437	0.480	0.00	−0.043	−0.14	0.432	+0.005	+0.01
B-F	0.411	0.478	+0.04	−0.067	−0.21	0.430	−0.019	−0.05
B-T	0.352	0.438	+0.07	−0.086	−0.19	0.394	+0.042	−0.08
E-H	0.650	0.658	0.00	−0.008	−0.03	0.592	+0.058	+0.17
E-F	0.589	0.654	0.00	−0.065	−0.25	0.589	0.000	0.00
E-T	0.526	0.600	0.00	−0.074	−0.20	0.540	−0.014	−0.03
H-F	0.898	0.868	0.00	+0.030	+0.23	0.781	+0.117	+0.53
H-T	0.859	0.796	0.00	+0.063	+0.34	0.717	+0.142	+0.52
F-T	0.944	0.792	+0.03	+0.152	+0.78	0.713	+0.231	+0.83

The primary correlation coefficients of the two populations differ greatly. Those of F_1 are mostly small. They seem rather erratic as expected from the large standard error. The much larger correlations in F_2 indicate a much greater role of general size factors and support CASTLE's view that most of the genetic variability is of this sort. However, on making the same sort of analysis as with MACDOWELL's rabbits, the minimized residuals and especially the deduced partial correlations for constant general size, come out astonishingly similar in F_1 and F_2. Only two of the 21 signs are different and even the values are for the most part closely similar. As in MACDOWELL's data, the residual correlations between head and leg measures are all negative. Again, it has seemed desirable to eliminate significant negative residuals by reducing the path coefficients. The same method was followed in this and in all other cases, that of equalizing the averages of the 4 correlations between head and hind leg measures in the observed and calculated data. In this case, the path coefficients were multiplied by 0.865, in the F_1 data, by 0.949 in F_2 to obtain the revised estimates. The correlation between the revised partial correlation coefficients of F_1 and F_2 comes out $+0.85 \pm 0.06$, indicating that the similarity of the residuals in these two populations can not be accidental.

Examination of the partial correlations indicates the existence of a head group including the ears as well as the length and breadth of the skull. Curiously enough, body weight appears to be associated with this group rather than with the legs. Moreover, it is not as strongly correlated with the general factor as are the leg bones and skull length. The leg bones form a second group with additional factors indicated for the hind leg bones. It will be seen that these indications agree qualitatively (as far as comparison can be made) with those from MACDOWELL's rabbits. There is a difference in the absence of any indication of a common factor for proximal long bones (humerus and femur) in addition to those for leg bones in general. There is also a little more indication than the negligible one in the MACDOWELL rabbits for a closer relation of humerus to head than of hind leg bones to head. The indications from the F_1 data are practically the same as from the F_2, except that they agree with the MACDOWELL rabbits in showing more residual relation between humerus and femur than between humerus and tibia. They go beyond the F_2 data in indicating a relationship of humerus to head measurements not shared by the hind legs. In both F_1 and F_2, much the highest residual correlation is that between femur and tibia.

Turning to the column pC in tables 3 and 5 for indications of heterogonic growth, it will be seen that F_1 and F_2 agree with each other but disagree with the MACDOWELL rabbits in that the skull measurements fall off rela-

tively to the leg measurements with increasing general size. The ears increase with the legs in the F_1 data but fall off slightly in F_2. Both agree with the MacDowell rabbits in the indication of increasing dolichocephaly with increasing size, the F_2 data showing this effect to an excessive extent. In this connection, it is of interest that the large race used was much more dolichocephalic than the small race. The great difference in ear lengths can not be due merely to heterogony. The means (in grams and mm) are given by Castle as follows:

	WEIGHT	L	B	E	H	F	T
Flemish giant	3646	85.5	45.4	14.5	75.0	97.6	110.0
Polish	1404	65.7	38.0	8.4	57.7	72.3	83.9
Ratio	2.60	1.30	1.20	1.74	1.30	1.35	1.32

A possibility which must be considered is that sex differences are responsible for the residual correlations in whole or part. There were 13 females and 14 males in the F_1 group and 52 females, 60 males among the F_2's. It happens, however, as Castle points out, that the sex differences in rabbits are small. The females were slightly heavier, there was no appreciable difference in length of skull or ear length, while the males were slightly longer legged and broader headed. It is possible to calculate the variance due to sex by the formula $q(1-q)\Delta^2$ where q is the proportion of males and Δ is the average sex difference. The ratio of the square root of this quantity, to the total standard deviation, with the sign of the sex difference gives the path coefficient measuring the influence of sex on the character. The products of these in pairs give the contribution to the various correlations and are given in tables 4 and 6. It will be seen that sex differences are not responsible for the important residuals. In fact the signs are in many cases the reverse of those of the calculated residuals which thus would take on added significance if corrected for sex.

ANALYSIS OF MEASUREMENTS OF FOWLS

Dunn (1928) has published a long series of bone measurements of hens from a White Leghorn flock which is well adapted to the present method of analysis. The records of many of the birds were incomplete but complete sets of measurements of length and breadth of skull, and lengths of humerus, ulna, femur and tibia, were available for 276 hens. Again it seemed desirable to restrict the data to complete records and all constants and correlations were recalculated for these alone. Length and breadth of skull were tabulated in 0.4 mm intervals (26.8–27.1, etc.), humerus, ulna

and femur in 1 mm intervals (57.0–57.9, etc.) and tibia in 2.0 mm intervals (96.0–97.9, etc.).

The results did not differ to any important extent from those which were reported by DUNN who, however, gave only a few of the correlations.

TABLE 7

Statistics of 276 White Leghorn hens, calculated from the data of DUNN *(1928). Symbols as in table 1.*

	MEAN	SD	C	p	pC
L (skull length)	38.77	1.26	3.25	0.665	2.16
B (skull breadth)	29.81	0.93	3.13	0.615	1.92
H (humerus)	74.64	2.84	3.80	0.953	3.62
U (ulna)	68.74	2.73	3.97	0.942	3.74
F (femur)	77.34	3.20	4.14	0.923	3.82
T (tibia)	114.84	5.00	4.35	0.942	4.10

TABLE 8

Analysis of correlations between measurements of hens, described in table 7. Symbols as in table 2,
$$p'_{1G}p'_{2G}=0.943p_{1G}p_{2G}.$$

	r	P1GP2G	Δ	r₁₂.G	P'1GP'2G	Δ'	r'₁₂.G
L-B	0.584	0.409	+0.175	+0.30	0.385	+0.199	+0.32
L-H	0.615	0.634	−0.019	−0.08	0.598	+0.017	+0.06
L-U	0.601	0.626	−0.025	−0.10	0.590	+0.011	+0.04
L-F	0.570	0.614	−0.044	−0.15	0.579	−0.009	−0.03
L-T	0.600	0.626	−0.026	−0.10	0.590	+0.010	+0.03
B-H	0.576	0.586	−0.010	−0.04	0.553	+0.023	+0.08
B-U	0.530	0.579	−0.049	−0.18	0.546	−0.016	−0.05
B-F	0.526	0.568	−0.042	−0.14	0.536	−0.010	−0.03
B-T	0.555	0.579	−0.024	−0.09	0.546	+0.009	+0.03
H-U	0.940	0.898	+0.042	+0.41	0.847	+0.093	+0.61
H-F	0.875	0.880	−0.005	−0.04	0.830	+0.045	+0.27
H-T	0.878	0.898	−0.020	−0.20	0.847	+0.031	+0.20
U-F	0.877	0.869	+0.008	+0.06	0.819	+0.058	+0.32
U-T	0.886	0.887	−0.001	−0.01	0.836	+0.050	+0.31
F-T	0.924	0.869	+0.055	+0.43	0.819	+0.105	+0.59

Exactly the same method of analysis was followed as before, including revision of the contributions of the postulated general factor so as to make the average residual of the 4 correlations between head and leg measurements zero. The conclusions (tables 7 and 8) are clear cut and present much the same picture as the 3 rabbit populations. The most important factor is general in action, but the head measurements constitute a group with a common factor determining about 20 percent of their variances. The leg and wing measurements depend on a common factor, not operative on the

head, which determines 4 to 6 percent of their variances. There is an additional common factor for the two wing bones, and also such a factor for the two leg bones which in each case brings the portion of the variance determined jointly up to 9 to 12 percent. There are, however, no indications of joint variability of the homologous bones of the wings and legs independently of the non-homologous bones.

ANALYSIS OF VARIANCE

Table 9 gives a summary of the percentage analysis of the variance by general, group and special factors for the four bodies of data. Only those group factors are recognized here which seem best established. The indication of joint variability in humerus and femur and the relationship of the humerus to the head measurements are ignored, requiring a slight modification of the estimates previously given. These figures bring out the great importance of general size factors (except in the F_1 rabbits) emphasized by CASTLE and also the consistency with which certain group factors are indicated. These percentages are translated into actual variance in the last four columns.

The comparison of the F_1 and F_2 variances throws some light on the question as to how far the various factors are genetic. A large part of the F_1 variance may be environmental, but at least the excess variance in F_2 must be interpreted as genetic due to segregation. The enormous increase in variance in F_2 due to the general factor is apparent. There is also, however, an increase in every case in the variance attributed to the group and special factors. This indicates that genetic factors are involved here also. In the case of DUNN's fowls, he was able to show that special genetic factors were affecting the ratio of the two skull measurements, of the two wing measurements and of the two leg measurements. He found that different ratios came to be characteristic of different inbred strains.

In concluding this analysis, the reader may feel that a somewhat involved procedure has merely brought out relations which might have been anticipated by anyone in advance. To this it may be said that the naturalness and consistency of the groupings yielded by the analysis give evidence of the validity of a method which in other cases may bring to light more unexpected results and that in any case it is desirable to substitute quantitative determinations for vague opinions.

SUMMARY

A method is developed of analyzing the system of all possible correlations among a number of measurements of parts of the body, by which one

TABLE 9

Analysis of variance, both in relative terms and in absolute terms, of measurements of 3 rabbit populations and one hen population. Indication of grouping of humerus with head group (9 percent in F_1 rabbits, 3 percent in F_2 rabbits) ignored. Also indication of grouping of humerus with femur to greater extent than with tibia.

| | PERCENTAGE OF VARIANCE DETERMINED | | | | ACTUAL VARIANCE DETERMINED | | | |
| | RABBITS | | | HENS | RABBITS | | | HENS |
	F_1	F_2	M		F_1	F_2	M	
Weight								
General	9	55	..	..	5	79	..	..
Head group	19	11	..	..	11	16	..	..
Special	72	34	..	..	40	49	..	..
Ear length								
General	13	45	..	..	1.5	13.5	..	..
Head group	18	13	..	..	2.1	13.9	..	..
Special	69	42	..	..	8.2	12.6	..	..
Skull length								
General	40	65	68	42	1.2	11.5	16.5	4.4
Head group	12	8	11	19	0.4	1.4	2.7	2.0
Special	48	27	21	39	1.5	4.8	5.1	4.1
Skull breadth								
General	13	24	57	36	0.7	2.0	10.3	3.5
Head group	18	18	15	20	1.1	1.5	2.7	2.0
Special	69	58	28	44	4.0	4.7	5.1	4.3
Humerus								
General	47	78	77	86	1.5	16.3	12.0	12.4
Limb group	11	12	5	4	0.3	2.5	0.8	0.6
Forelimb group	..	..	..	5	..	..	..	0.7
Special	42	10	18	5	1.3	2.1	2.8	0.7
Ulna								
General	..	..	..	84	..	..	..	13.2
Limb group	..	..	..	4	..	..	..	0.6
Forelimb group	..	..	..	6	..	..	..	0.9
Special	..	..	..	6	..	..	..	0.9
Femur								
General	51	78	83	80	2.0	17.4	11.6	13.7
Limb group	11	11	4	6	0.4	2.5	0.6	1.0
Hind limb group	28	7	3	6	1.1	1.6	0.4	1.0
Special	10	4	10	8	0.4	0.9	0.4	1.4
Tibia								
General	27	65	73	84	1.5	17.2	9.1	15.9
Limb group	16	18	6	4	0.9	4.8	0.8	0.8
Hind limb group	42	11	4	5	2.4	2.9	0.5	0.9
Special	15	6	17	7	0.8	1.6	2.1	1.3

may find the maximum effect compatible with the data which can be assigned to a general size factor, and determine the nature and degree of influence of residual group and special factors. The method is applied to published data on 3 populations of rabbits including F_1 and F_2 of a cross between breeds at opposite extremes in size, and to data on White Leghorn fowls. In all of these (except the F_1 rabbits) the influence of general size factors preponderates, but the residuals indicate the existence of group factors for the head apart from general size, of group factors for the forelimbs and hind limbs collectively, for the hind limbs separately and for the wings in fowls, the only case in which two fore limb measurements were available. Special factors acting on each part separately from the others are also indicated. The genetic differences in the rabbit case were largely in general size but to a small extent in group and special factors.

LITERATURE CITED

CASTLE, W. E., 1914 The nature of size factors as indicated by a study of correlation. Pub. Carnegie Instn. **196**: 51–55.

1922 Genetic studies of rabbits and rats. Pub. Carnegie Instn. **320**: 1–55.

1923 Does the inheritance of differences in general size depend upon general or special size factors? Proc. Nat. Acad. Sci. Washington **10**: 15–22.

1924a Are the various parts of the body genetically independent in size? Proc. Nat. Acad. Sci. Washington **10**: 181–182

1924b Consequences of race crossing, J. Hered. **15**: 363–369.

1929 A further study of size inheritance with special reference to the existence of genes for size characters. J. Exp. Zool. **53**: 421–454.

CASTLE, W. E. and GREGORY, P. W., 1929 The embryological basis of size inheritance in the rabbit. J. Morph. and Physiol. **48**: 81–102.

DAVENPORT, C. B., 1917 The inheritance of stature. Genetics **2**: 313–389.

DUNN, L. C., 1928 The effect of inbreeding on the bones of the fowl. Storrs Agric. Expt. Sta. Bull. **152**: 1–112.

GREEN, C. V., 1931a On the nature of size factors in mice. Amer. Nat. **65**: 406–416.

1931b Linkage in size inheritance. Amer. Nat. **65**: 502–507.

GREGORY, P. W. and CASTLE, W. E., 1931 Further studies on the embryological basis of size inheritance in the rabbit. J. Exp. Zool. **59**: 199–211.

HUXLEY, J. S., 1929 The existence and importance of growth gradients. Biol. Zbl. **49**: 490–493.

MACDOWELL, E. C., 1914 Size inheritance in rabbits. Pub. Carnegie Instn. **196**: 7–49.

MJOEN, J. H., 1923 Harmonic and disharmonic race crossings. Eugenics in Race and State. Proc. Second Inter. Congress of Eugenics. **2**: 41–61. Baltimore: Williams and Wilkins.

SUMNER, F. B., 1923 Size factors and size inheritance. Proc. Nat. Acad. Sci. Washington **9**: 391–397.

1924 The partial genetic independence in size of the various parts of the body. Proc. Nat. Acad. Sci. Washington **10**: 178–180.

WRIGHT, S., 1918 On the nature of size factors. Genetics **3**: 367–374.