ON THE NATURE OF SIZE FACTORS

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In a recent paper on the inheritance of stature in man, DAVENPORT (1917) discusses the relative importance of factors which affect the growth of the body as a whole and factors which affect only particular parts. He finds the latter more important in his data. He quotes results of CASTLE and of PEARSON in which the reverse was the case. The present paper is a further study of Prof. CASTLE's results, designed to illustrate a method of analysis as well as to bring out certain conclusions.

CASTLE (1914) gives all the correlations between five bone measurements in a stock of rabbits. He used length and breadth of skull, and lengths of humerus, femur and tibia. The measurements were those taken by MACDOWELL (1914) in his study of the inheritance of size in rabbits and are described by him in detail. This stock of rabbits was, unfortunately for the present purpose, of a rather heterogeneous character. It includes the offspring of a cross between a large and a small race and the back-cross of these with the small race. The inclusion of these two groups would tend to exaggerate the apparent importance of general size factors.

Both sexes are also combined. In three of the measurements this makes no appreciable difference. The average differences for length and width of skull and length of humerus were .001 cm, .031 cm and .007 cm, respectively, in favor of the females. The males, however, had distinctly longer hind legs. The average excess was .392 cm for the femur and .321 cm for the tibia. Thus the influence of sex must be taken into account where femur and tibia are involved.

In the following table, CASTLE's ten original correlations are given in the first column. The probable errors are small owing to the large size of the correlations as well as to the number of observations (between 370 and 380 in all cases). The five following columns give all the correlations between measurements for samples in which a third measurement is constant. These were calculated by PEARSON's familiar formula for correlation between a and b for constant c, ${}_cR_{ab} = \dfrac{r_{ab} - r_{ac}r_{bc}}{\sqrt{(1-r^2_{ac}) \times (1-r^2_{bc})}}$. The next ten columns give all the correlations for samples in which two measurements are constant, while the last column gives the correlations with three measurements constant. In the table OM is length of skull (occipital to maxilla), Zp is width of skull (posteriorly across the zygomatic arch), and H, F and T are the lengths of humerus, femur and tibia.

	r	OM^R	Zp^R	H^R	F^R	T^R	$OM\text{-}Zp^R$	$OM\text{-}H^R$	$OM\text{-}F^R$	$OM\text{-}T^R$
$OM\text{-}Zp$	.750 ± .015	. . .	. . .	.502	.496	.538	. . .	.	. .	. . .
H	.743 ± .016	. . .	.485	. . .	.275	.431	. . .	. . .	.	. . .
F	.760 ± .015	. . .	.519	.356	. . .	.432	. . .	. . .	. . .	. . .
T	.701 ± .018		.416	.276	.147	. .	. . .			.
$Zp\text{-}H$	.675 ± .019	.266	. . .		.254	.334	. . .	.	.145	.135
F	.674 ± .019	.242	. . .	.250	. . .	.282	.	.088		.067
T	.658 ± .020	.280		.275	.211	. .	. . .	.162	.160	
$H\text{-}F$	.857 ± .009	.671	.737	. .	. . .	.567	.649	. . .	. .	.467
T	.791 ± .013	.566	.628	. . .	.211	.	.531	. . .	.181	. . .
$F\text{-}T$	.858 ± .009	.700	.746	.571		. . .	.679	.524	. .	. . .

	$Zp\text{-}H^R$	$Zp\text{-}F^R$	$Zp\text{-}T^R$	HF^R	HT^R	FT^R	R (three constant factors)
$OM\text{-}Zp$	. . .	. . .	. . .	.456	.502	.481	.448
H	. . .	.176	.316	. . .	. . .	.252	.172
F	.274	. . .	.345	. .	.251	. . .	.224
T	.163	.051	.	.095		.	.022
$Zp\text{-}H$	. . .	. . .	. . .	.		.218	.119
F	. . .	. . .	. . .	. .	.118	.	.004
T	. . .		. . .	.166		.	.136
$H\text{-}F$	. . .	.	.517	. .	. .	. .	.463
T	. . .	.173	. . .	.	.	.	.161
$F\text{-}T$	.537	. .	. .	. . .	.	. . .	.517

The strikingly high correlations between skull and leg measurements were noted by CASTLE as evidence of the overwhelming importance of *general* factors for growth in this stock of rabbits.

Inspection of the primary correlations in the table shows that skull width (Zp) has very much more independent variability than the length of the skull (OM) and that the length of the tibia (T) has more independent variability than the length of humerus (H) or femur (F).

For further analysis, a study of the correlations with three measurements constant is very instructive. Such a population of rabbits should be nearly free from variations due to general size factors. Calculation shows that with 75 percent of the variation (as measured by squared standard deviation) due to general size factors in the original population, only about 23 percent should be due to such factors within a sample in which three measurements are constant.

Inspection of the ten correlations with three factors constant (last column) shows that all are positive but only three exceed .22. Length and breadth of skull have a correlation of .45 even though all three leg bones are constant. Humerus and femur (homologous bones of different limbs) have a correlation of .46 when both skull measurements and *tibia* are constant and finally femur and tibia (bones of the same limb) have a correlation of .52, although both skull measures and *humerus* are constant. These three correlations suggest the existence of growth factors which affect the size of the skull independently of the body, others which affect similarly the length of homologous long bones apart from all else, and others which affect similarly bones of the same limb. In the last case we know directly of one factor, viz., sex, as has already been stated. It is to be noted especially that humerus and tibia (non-homologous and on different limbs) show very little correlation (.16) when the skull measures and *femur* are constant. Indeed the correlation is very small (.21) when the femur is the only constant measurement. The low correlation between a skull dimension and a leg bone when the other skull dimension and one or both of the other leg bones is constant, is not surprising. It is hardly worth considering the differences in magnitude of these small correlations ranging from .00 to .22 but it may be noted that there are slight indications that brachicephaly is associated with long tibia but short femur.

The correlations with two constant measures bear out the previous results in all respects. The only other point which need be noted is that humerus and tibia show considerable correlation (.53) when both skull measures are constant. This is in harmony with correlation found between the head measures with all three leg bones constant, indicating the existence of separate factors for growth of skull and growth of the rest of the body. The correlations with one constant factor fall in line with the interpretation already cited but give less clear-cut results owing to the larger part played by general growth factors. It is worth noting that the femur seems to be the most closely related to general growth of any of the measurements, while the width of the skull is the least. All of the original correlations are over .65. On making the femur constant all but one are reduced to below .28 while that one, the correlation between length and breadth of skull, falls from .750 to .496. On the other hand when the skull breadth is constant, no correlation falls below .41 and the correlations between the long bones are all over .62.

It is of interest to attempt to assign definite values to the different classes of growth factors which are indicated. The following kinds may conveniently be distinguished, granting, of course, that no sharp lines can really be drawn.

Factors which affect:

a. General size (all parts of the skeleton alike).
b. Size of skull only, but all skull bones alike.
c. Length of leg bones only, but these alike.
d. Length of bones of hind limbs only, but these alike.
e. Length of homologous leg bones only, but these alike.
f. Each part independently.

A rough analysis can be made by use of the following proposition. Let X and Y be two characters whose variations are determined in part by certain causes A, B, C, etc., which act on both and in part by causes which apply to only one or the other, M and N respectively. These causes are assumed to be independent of each other. Represent by small letters, a, b, c, etc., the proportions of the variation of X determined by these causes and by a^1, b^1, c^1, etc., the proportions in the case of Y. The extent to which a cause determines the variation in an effect is measured by the proportion of the squared standard deviation of the latter for which it is responsible. This follows from the proposition that the squared standard deviations due to single causes acting alone may be combined by simple addition to find the squared standard deviation of an array in which all causes are acting, provided the causes are independent of each other, i.e., $\sigma^2_{A+B+C} = \sigma^2_A + \sigma^2_B + \sigma^2_C$.

Effects	Causes					
	A	B	C	D	M	N
X	a	b	c	d	m	
Y	a^1	b^1	c^1	d^1		n^1

As a, b, etc., are the proportions of the variation of X which are determined by the various causes

$$a + b + c + d \ldots\ldots + m = 1$$
$$a^1 + b^1 + c^1 + d^1 \ldots\ldots + n^1 = 1$$

It is easy to demonstrate the following proposition in regard to the correlation between X and Y.

$\therefore r_{xy} = \pm\sqrt{aa^1} \pm \sqrt{bb^1} \pm \sqrt{cc^1} \ldots$

Where a given cause as A produces effects in the same direction in X and Y the sign of the term $\sqrt{aa^1}$ is +. Where the effects are in opposite directions the sign is —.

Applying this method to the rabbit data, the following factors may be distinguished.

Growth factors

Variations in	General	Skull	Legs	Hind legs	Proximal leg bones	Special
OM	a	b	....	....	....	m
Zp	a^{I}	b^{I}	....	....	....	n^{I}
H	a^{II}	..	c^{II}	....	e^{II}	o^{II}
F	a^{III}	..	c^{III}	d^{III}	e^{III}	p^{III}
T	a^{IV}	..	c^{IV}	d^{IV}	......	q^{IV}

The ratios of a^{I} to a and of a^{IV} and a^{III} to a^{II} are easily calculated.

(1) $r^2_{OM\text{-}H} = aa^{II} = .5520$
(2) $r^2_{Zp\text{-}H} = a^{I}a^{II} = .4556$
(3) $r^2_{OM\text{-}F} = aa^{III} = .5776$
(4) $r^2_{Zp\text{-}F} = a^{I}a^{III} = .4543$
(5) $r^2_{OM\text{-}T} = aa^{IV} = .4914$
(6) $r^2_{Zp\text{-}T} = a^{I}a^{IV} = .4330$

The three values of $\frac{a^{I}}{a}$ derived by dividing (2) by (1), (4) by (3) and (6) by (5) are .8254, .7865 and .8812, with an average of .8310. Thus general growth is only 83 percent as important in determining variation of the width of the skull as it is in determining variations in skull length. By dividing (3) by (1) and (4) by (2) we get two values of $\frac{a^{III}}{a^{II}}$, 1.0464 and .9971, with an average of 1.0218. By dividing (5) by (1) and (6) by (2) we get two values of $\frac{a^{IV}}{a^{II}}$, .8902 and .9504, with an average of .9203. Thus as regards the proportion of their variation determined by general growth factors,

$$Zp : OM = .8310 : 1.0000$$
$$T : F : H = .9203 : 1.0218 : 1.0000$$

The skull measurements cannot be compared with the leg measurements without further assumptions. The following results are of use in this connection:

$$_HR_{OM\text{-}Zp} = \frac{r_{OM\text{-}Zp} - \sqrt{aa^{II}}\sqrt{a^I a^{II}}}{\sqrt{(1-r^2_{OM\text{-}H})(1-r^2_{Zp\text{-}H})}} = .502 \therefore \sqrt{aa^I} = \frac{.5021}{a^{II}},$$

$$_FR_{OM\text{-}Zp} = \frac{r_{OM\text{-}Zp} - \sqrt{aa^{III}}\sqrt{a^I a^{III}}}{\sqrt{(1-r^2_{OM\text{-}F})(1-r^2_{Zp\text{-}F})}} = .496 \therefore \sqrt{aa^I} = \frac{.5010}{a^{II}},$$

$$_TR_{OM\text{-}Zp} = \frac{r_{OM\text{-}Zp} - \sqrt{aa^{IV}}\sqrt{a^I a^{IV}}}{\sqrt{(1-r^2_{OM\text{-}T})(1-r^2_{Zp\text{-}T})}} = .538 \therefore \sqrt{aa^I} = \frac{.5010}{a^{II}}.$$

$\sqrt{aa^I} = \frac{.5014}{a^{II}}$ as the average of three determinations. Similarly from $_{OM}R_{HT}$ and $_{Zp}R_{HT}$ we get $\sqrt{a^{II}a^{IV}} = \frac{.5208}{a}$ or $\frac{.5320}{a}$, with $\sqrt{a^{II}a^{IV}} = \frac{.5264}{a}$ as the average of two determinations. Now $\sqrt{aa^I}$ cannot exceed $r_{OM\text{-}Zp}$ (which equals $\sqrt{aa^I} + \sqrt{bb^I}$). The maximum value, $\sqrt{aa^I} = .750$, is on the assumption that $\sqrt{bb^I} = 0$. Similarly $\sqrt{a^{II}a^{IV}}$ can have the maximum value .791 but only on the assumption that $\sqrt{c^{II}c^{IV}} = 0$.

As $a^I = .831\, a$, $\sqrt{aa^I} = a\sqrt{.831}$,

and the maximum value of a is therefore $\frac{.750}{\sqrt{.831}} = .823$.

Similarly the maximum value of a^{II} is $\frac{.791}{\sqrt{.920}} = .825$

From the equation $\sqrt{aa^I} = \frac{.5014}{a^{II}}$, the minimum value of $\sqrt{aa^I}$ is evidently $\frac{.5014}{.825} = .609$ (assuming $\sqrt{c^{II}c^{IV}} = 0$), and similarly the minimum value of $\sqrt{a^{II}a^{IV}}$ is $\frac{.5264}{.825} = .638$ (assuming $\sqrt{bb^I} = 0$).

These maximum and minimum possible values can be tabulated thus:

	No general skull factors ($\sqrt{bb^I} = 0$)	No general leg factors ($\sqrt{c^{II}c^{IV}} = 0$)
$\sqrt{aa^I}$	.750	.609
$\sqrt{a^{II}a^{IV}}$	.638	.791

The partial correlation between length and width of skull for constant humerus, femur and tibia ($_{H\text{-}F\text{-}T}R_{OM\text{-}Zp} = .448$), shows clearly that there are factors for skull size affecting length and breadth alike, while the partial correlation between humerus and tibia for constant length and width of skull (${}_{OM\text{-}Zp}R_{H\text{-}T} = .531$), shows that there are factors affecting the leg bones in common. Thus neither of the extreme assumptions, $\sqrt{bb^{I}} = 0$ and $\sqrt{c^{II}c^{IV}} = 0$, is tenable. The assumption that $\sqrt{aa^{I}}$, has a value about half way between the extremes .750 and .609,—viz., .679, should give satisfactory results. On this basis $a = .746$ and a^{I}, a^{II}, a^{III} and a^{IV} are easily calculated.

$$a = .746 \qquad \sqrt{aa^{I}} = .679$$

$$a^{I} = .746 \times .831 = .620 \qquad \sqrt{a^{II}a^{IV}} = .707$$

$$a^{II} = \frac{.5014}{.679} = .738$$

$$a^{III} = .738 \times 1.022 = .754$$

$$a^{IV} = .738 \times .920 = .679$$

As $r_{OM\text{-}Zp} = \sqrt{aa^{I}} + \sqrt{bb^{I}} = .750$,

$\sqrt{bb^{I}} = .750 - .679 = .071$ (maximum $= .141$, minimum $= 0$).

As $r_{HT} = \sqrt{a^{II}a^{IV}} + \sqrt{c^{II}c^{IV}} = .791$,

$\sqrt{c^{II}c^{IV}} = .791 - .707 = .084$ (minimum $= 0$, maximum $= .153$).

As $r_{HF} = \sqrt{a^{II}a^{III}} + \sqrt{c^{II}c^{III}} + \sqrt{e^{II}e^{III}} = .857$,

$\sqrt{c^{II}c^{III}}$ cannot differ much from $\sqrt{c^{II}c^{IV}}$, and .080 should be a fair estimate.

Thus $\sqrt{e^{II}e^{III}} = .857 - .747 - .080 = .030$

Similarly $r_{FT} = \sqrt{a^{III}a^{IV}} + \sqrt{c^{III}c^{IV}} + \sqrt{d^{III}d^{IV}} = .858$. Assigning the value .080 to $\sqrt{c^{III}c^{IV}}$ we get $\sqrt{d^{III}d^{IV}} = .858 - .717 - .080 = .061$.

The following table is derived from these results.

Relative importance of different classes of size factors of five bone lengths.

	General size	Skull	Legs	Hind legs	Proximal leg bones	Special	Total
OM	.746	.077	....	....	....	.177	1.0000
Zp	.620	.065	....	....	....	.315	1.0000
H	.739	....	.083	....	.030	.148	1.0000
F	.755	....	.085	.064	.030	.066	1.0000
T	.680	....	.076	.058	....	.186	1.0000

SUMMARY

Analysis of the relations between five bone lengths in a population of rabbits shows that most differences between individuals are those which

involve the size of the body as a whole. There is, however, a certain amount of variation of each bone length independently of all others measured and there are also groups of bones which vary together independently of the rest of the body. Skull length and breadth on one hand, and the three leg bones on the other, are two such groups. Again the bones of the hind leg, femur and tibia, form a group subject to common influences which do not affect the humerus, a bone of the foreleg, and finally femur and humerus, homologous bones in hind and foreleg, vary together independently of the tibia. A mode of estimating the relative importance of these different kinds of growth factors is presented and applied to the rabbit data.

LITERATURE CITED

CASTLE, W. E., 1914 The nature of size factors as indicated by a study of correlation. Carnegie Inst. Wash. Publ. No. 196, pp. 51-55.

DAVENPORT, C. B., 1917 Inheritance of stature. Genetics **2**: 313-389.

MAC DOWELL, E. C., 1914 Size inheritance in rabbits. Carnegie Inst. Wash. Publ. No. 196, pp. 7-49.