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Further Remarks on the Law of Ancestral Heredity

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V. Further Remarks on the Law of Ancestral Heredity*.

By KARL PEARSON, F.R.S.

This law is a *rule* for predicting the *average* value of a character in the offspring of ancestry with given characters.

It is based on the following assumptions:

- (i) The proper prediction formula is the multiple regression formula.
- (ii) The individual ancestors in any generation may be replaced by the mid-ancestor of this generation, i.e. an individual supposed to have, as his character, that linear function of the characters of all the ancestors in that generation which is most highly correlated with the character of the offspring.
- (iii) The individual ancestral correlations decrease in geometrical progression. This is very close to the truth in practically all the races that have been statistically investigated.

The general multiple regression formulae are

$$x_0 - \bar{x}_0 = S \left\{ c_p \frac{\sigma_0}{\Sigma p} (X_p - \bar{X}_p) \right\} \dots\dots\dots(i),$$

$$\Sigma p = \sigma_0 \sqrt{1 - S(c_p r_{p0})} \dots\dots\dots(ii),$$

where X_p is the character of the p th mid-ancestor, r_{p0} the correlation of this ancestor and the offspring, while

$$\Sigma p = \frac{\sigma_p}{2^{\frac{1}{2}p}} \sqrt{1 + \epsilon_p} \dots\dots\dots(iii),$$

$$r_{p-q} = 2^{\frac{1}{2}(p-q)} \rho_{p-q} / \sqrt{(1 + \epsilon_p)(1 + \epsilon_q)} \dots\dots\dots(iv),$$

where ϵ_p is the assortative mating in the p th generation, σ_p is the variability of that generation and ρ_{p-q} = average correlation of the *individual* p th ancestor with the offspring of the q th generation.

Further we have to determine the c 's

$$\left. \begin{aligned} r_{01} &= c_1 + c_2 r_{12} + c_3 r_{13} + \dots + c_n r_{1n} \\ r_{02} &= c_1 r_{21} + c_2 + c_3 r_{23} + \dots + c_n r_{2n} \\ r_{03} &= c_1 r_{31} + c_2 r_{32} + c_3 + \dots + c_n r_{3n} \end{aligned} \right\} \dots\dots\dots(v).$$

Assume $r_{pq} = a\beta^{p-q}$, which will clearly be the case if ρ_{p-q} is of the form

$$\zeta \theta^{p-q} \dots\dots\dots(vi),$$

or in accord with our condition (iii). We shall show that $c_p = \gamma \eta^p$ satisfies the above equations.

Substituting we have

$$\left. \begin{aligned} a\beta &= \gamma (\eta + \eta^2 a\beta + \eta^3 a\beta^2 + \dots) \\ a\beta^2 &= \gamma (\eta a\beta + \eta^2 + \eta^3 a\beta + \dots) \\ a\beta^3 &= \gamma (\eta a\beta^2 + \eta^2 a\beta + \eta^3 + \dots) \end{aligned} \right\} \dots\dots\dots(vii).$$

* Reproduced from lecture notes on multiple regression.

Or, supposing the ancestry to ascend indefinitely by the same law,

$$\left. \begin{aligned} a\beta &= \gamma \left(\eta + \frac{\eta^2 a\beta}{1 - \eta\beta} \right) \\ a\beta^2 &= \gamma \left(\eta a\beta + \eta^2 + \frac{\eta^3 a\beta}{1 - \eta\beta} \right) \\ a\beta^3 &= \gamma \left(\eta a\beta^2 + \eta^2 a\beta + \eta^3 + \frac{\eta^4 a\beta}{1 - \eta\beta} \right) \end{aligned} \right\} \dots\dots\dots(\text{viii}).$$

Multiply each equation by η and subtract it from the one below it. We find

$$\left. \begin{aligned} a\beta(\beta - \eta) &= \gamma\eta a\beta \\ a\beta^2(\beta - \eta) &= \gamma\eta a\beta^2 \\ \dots\dots\dots &= \dots\dots\dots \end{aligned} \right\} \dots\dots\dots(\text{ix})$$

or

$$\beta - \eta = \gamma\eta \text{ in each case}$$

Substitute this value of $\gamma\eta$ in the first equation and we have

$$\left. \begin{aligned} a\beta &= (\beta - \eta) \left(1 + \frac{\eta a\beta}{1 - \eta\beta} \right) \\ a\beta &= \frac{(\beta - \eta)(1 - \eta\beta)}{\eta^2 - 2\eta\beta + 1} \end{aligned} \right\} \dots\dots\dots(\text{x}).$$

Hence

$$\Sigma = \sigma_0 \sqrt{1 - S(\gamma a(\eta\beta)^p)} = \sigma_0 \sqrt{1 - \frac{\gamma a\eta\beta}{1 - \eta\beta}} = \sigma_0 \sqrt{1 - \frac{(\beta - \eta)^2}{\eta^2 - 2\eta\beta + 1}} = \sigma_0 \sqrt{\frac{1 - \beta^2}{\eta^2 - 2\eta\beta + 1}} \dots\dots(\text{xi}),$$

which determines the variability of the array with given ancestry.

Returning to Equation (x) we have

$$\eta^2 - \frac{\eta(1 - 2a\beta^2 + \beta^2)}{\beta(1 - a)} + 1 = 0,$$

or

$$\eta^2 - \eta\lambda + 1 = 0,$$

$$\eta = \frac{\lambda \pm \sqrt{\lambda^2 - 4}}{2} \dots\dots\dots(\text{xii}),$$

where it is necessary to take the root less than unity.

Application I. Galton's Rule. Sir Francis Galton took the "contributions" of each generation of ancestry to be $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \frac{1}{16}, \dots$. Thus each parent contributed on an average $\frac{1}{4}$, each grandparent $\frac{1}{8}$, each great-grandparent $\frac{1}{16}$, etc.

Our equation, if we neglect assortative mating, is

$$\begin{aligned} x_0 - \bar{x}_0 &= \frac{1}{2}(X_1 - \bar{X}_1) + \frac{1}{4}(X_2 - \bar{X}_2) + \dots \\ &= S \left\{ c_p \frac{\sigma_0}{\Sigma_p} (X_p - \bar{X}_p) \right\} \\ &= S \{ \gamma (\sqrt{2}\eta)^p (X_p - \bar{X}_p) \}, \end{aligned}$$

if we put $\sigma_p = \sigma_0$, i.e. suppose population stable.

$$\therefore \gamma = 1, \quad \sqrt{2}\eta = \frac{1}{2},$$

or by (ix)

$$\beta = 2\eta = 1/\sqrt{2}.$$

Therefore by (x)

$$a = \frac{\beta - \eta}{\beta} \frac{(1 - \eta\beta)}{\eta^2 - 2\eta\beta + 1} = \frac{1}{2} \frac{\frac{1}{2}}{\frac{1}{2}} = \frac{1}{2}.$$

Thus the mid-parental correlation $= a\beta^p = \frac{1}{2} \left(\frac{1}{\sqrt{2}} \right)^p$.

The individual ancestral correlations are found from

$$r_{p-q} = 2^{\frac{1}{2}}(p-q) \rho_{p-q},$$

or

$$\begin{aligned} \rho_{p-q} &= \cdot 6 \left(\frac{1}{\sqrt{2}} \right)^{p-q} / (\sqrt{2})^{p-q} \\ &= \cdot 6 \left(\frac{1}{2} \right)^{p-q}. \end{aligned}$$

Hence the individual parental correlation is $\cdot 3$ and the geometrical ratio $\frac{1}{2}$.

It is thus clear that Galton's Rule is not absolutely consistent with the Mendelian somatic correlations $\frac{1}{3}$, $\frac{1}{3} \times \frac{1}{2}$, etc., ..., although it is not very far removed from them.

The variability of an array of brothers from same ancestry is found from (xi) to be

$$\cdot 8944\sigma_0,$$

or, the reduction in variability by continued selection will not exceed 11 %.

The correlation of brothers

$$\begin{aligned} R &= (\beta - \eta) / \sqrt{\eta^2 - 2\eta\beta + 1} \\ &= \cdot 4472. \end{aligned}$$

Application II. Suppose the individual ancestral correlations follow the simple Mendelian somatic relation $\frac{1}{3}$, $\frac{1}{3} \times \frac{1}{2}$, etc.

Then

$$\begin{aligned} r_{p-q} &= (\sqrt{2})^{p-q} \frac{2}{3} \times \frac{1}{2^{p-q}} \\ &= \frac{2}{3} \left(\frac{1}{\sqrt{2}} \right)^{p-q} \end{aligned}$$

Hence

$$a = \frac{2}{3}, \quad \beta = \frac{1}{\sqrt{2}} = \cdot 7071,$$

whence we deduce

$$\eta = \cdot 3100, \quad \gamma\eta = \cdot 3971.$$

Our series is therefore

$$x_0 - \bar{x}_0 = \cdot 5617 (x_1 - \bar{x}_1) + \cdot 2463 (x_2 - \bar{x}_2) + \cdot 1080 (x_3 - \bar{x}_3) + \cdot 0474 (x_4 - \bar{x}_4) + \text{etc.},$$

this giving slightly more influence to the parents and less to the ancestry than Galton's Rule.

The correlation of brothers is $\cdot 4896$, giving

$$\Sigma_0 = \sigma_0 \times \cdot 8720,$$

or a reduction of variability of about 13 %.

Not much stress, however, must be laid on these results for a single Mendelian unit character. They are the furthest from true linear regression of the mid-parent and theoretically only two grades of the character occur.

Application III. Suppose the correlations are given by the Mendelian gametic values $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, etc.

We have

$$r_{p-q} = (\sqrt{2})^{p-q} \times \left(\frac{1}{2} \right)^{p-q} = \left(\frac{1}{\sqrt{2}} \right)^{p-q}.$$

Hence

$$a = 1, \quad \beta = \frac{1}{\sqrt{2}}.$$

It follows that

$$\eta = 0, \quad \gamma\eta = \beta = \frac{1}{\sqrt{2}}.$$

Hence the prediction formula reduces to

$$x_0 - \bar{x}_0 = X_p - \bar{X}_p,$$

or the parents suffice to determine the offspring. This is in complete accordance with the Mendelian idea of the gametic parental constitution determining the offspring.

Application IV. Return now to the case of a continuous variable for which the law of ancestral heredity was first developed. Observation seems to show that we have nearly $\frac{1}{2}, \frac{1}{2} \times \frac{2}{3}, \frac{1}{2} \times (\frac{2}{3})^2$, etc.

Hence

$$r_{p-q} = (\sqrt{2})^{p-q} \frac{1}{2} \times (\frac{2}{3})^{p-q},$$

or

$$a = \frac{1}{2}, \quad \beta = \left(\frac{2\sqrt{2}}{3} \right) = .9428,$$

whence

$$\eta^2 - 2.12134\eta + 1 = 0,$$

$$\eta = .70712 = \frac{1}{\sqrt{2}}, \quad \gamma\eta = .2357,$$

$$\gamma = .3333, \quad \eta\sqrt{2} = 1.0000.$$

Thus the series becomes very nearly

$$x_0 - \bar{x}_0 = \frac{1}{3} (X_1 - \bar{X}_1 + X_2 - \bar{X}_2 + X_3 - \bar{X}_3 + \dots).$$

This result is noteworthy; it shows that with the values found, three generations would suffice to produce offspring with the full selected character.

Here every individual ancestor provides on the average *half* the contribution of the ancestor one grade closer and not one quarter as in Galton's Rule. Hence by continual selection, we could advance a character *beyond* the selected value. How far such a selection is possible we do not know. The correlation with other characters would probably introduce counteracting selection.

We have in this case

$$\Sigma_0 = \sigma_0 \sqrt{1 - R^2} = \sigma_0 \sqrt{1 - (.5773)^2},$$

whence the correlation for brother = .5773, and

$$\Sigma_0 = \sigma_0 \times .8165,$$

or we have an 18% reduction in variability by in-breeding.

Galton's Condition.

Galton made it a condition of his series that if *all* the ancestry were selected and of value h , the offspring should have the same deviation h .

$$\begin{aligned} \text{In our case} \quad x_0 - \bar{x}_0 &= \gamma \{ \eta\sqrt{2} (X_1 - \bar{X}_1) + (\eta\sqrt{2})^2 (X_2 - \bar{X}_2) + \text{etc.} \} \\ &= \gamma\eta\sqrt{2} h / (1 - \eta\sqrt{2}), \end{aligned}$$

if all the ancestry deviate by h . Hence

$$\gamma\eta\sqrt{2} / (1 - \eta\sqrt{2}) = 1.$$

This is the generalised Galton condition.

It is very doubtful, however, whether it ever holds. Supposing it to hold, we may select for n generations only, then

$$x - x_0 = \gamma \{ \eta\sqrt{2}h + (\eta\sqrt{2})^2 h + \dots + (\eta\sqrt{2})^n h \},$$

if the other mid-parents were non-selected.

$$\begin{aligned} \text{Hence the offspring } h' &= \frac{\gamma\eta\sqrt{2} / \{1 - (\eta\sqrt{2})^n\} h}{1 - \eta\sqrt{2}}, \\ h' &= h \{1 - (\eta\sqrt{2})^n\}, \end{aligned}$$

by the condition. Thus if $\eta\sqrt{2}$ differ at all from unity, we rapidly get the full effect of selection, i.e. offspring = h . If, however, we stop selection at the n th generation, we have for the offspring of this generation with in-breeding

$$\begin{aligned} x - x_0 &= \gamma [\eta\sqrt{2}h \{1 - (\eta\sqrt{2})^n\} + (\eta\sqrt{2})^2 h + (\eta\sqrt{2})^3 h + \dots + (\eta\sqrt{2})^{n+1} h] \\ &= \gamma \{ \eta\sqrt{2}h + (\eta\sqrt{2})^2 h + (\eta\sqrt{2})^3 h + \dots + (\eta\sqrt{2})^n h \} \\ &= \frac{\gamma\eta\sqrt{2}}{1 - \eta\sqrt{2}} \{1 - (\eta\sqrt{2})^n\} h \\ &= \{1 - (\eta\sqrt{2})^n\} h = h', \end{aligned}$$

or, if selection be stopped at any stage, there will on in-breeding be *no* regression.

It is a remarkable fact that many biologists have accepted Galton's theory of regression, without seeing that there is no regression whatever on Galton's hypothesis after the first generation, at which selection is stopped! This misunderstanding arises from the common belief that a word carries its own definition and that it is not needful to study its algebraical significance.

Looked at as a whole it appears to me that the theory of multiple correlation is the natural manner in which to approach the theory of ancestral inheritance. The work done on man shows that for all sorts of types of measurable characters we have true linear regression, and that our correlations of *measurable* characters in all species hitherto dealt with are singularly constant. Further these correlations appear for the same grades of relationship to be the same for measurable and non-measurable characters. We are largely compelled to measure ancestral correlations by colour characters as no other data are available, but the equality of pigmental and of measurable-character correlations for grades we can compare gives us confidence in testing the decadence of resemblance on pigmental characters. And the law of geometrical decadence being once established we have a multiple regression formula which may be legitimately applied to all measurable characters.

The fact that the Mendelian gametic correlations approach in some respects those found by observation on populations, is not a justification of Mendelism. It is only an indication that for such special cases as "unit" characters, even if they exist, there is no absurdity in our geometrical law of decadence. Most biometricians, however, who have measured and observed characters in man or animals have not been able to classify into *A* and not-*A*, but believe that there are many grades of *A* and not-*A* and that probably every one of these are capable of selection and of inheritance. Thus they look to continuous or at least multiple variations of the germ-plasm with regard to any single character, and not to the mere presence or absence of a *single* determinant.

LITERATURE.

F. Galton : *Natural Inheritance*, 1889, pp. 133, 135—7.

Galton's correlation values (parental $\frac{1}{2}$, grandparental $\frac{1}{4}$, etc.) are not in accord with wider observation, and they are opposed to the $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, etc. of his own law of "contributions."

K. Pearson : *On the Law of Ancestral Heredity*, *Royal Soc. Proc.* Vol. 62, 1898, pp. 386—412.

This is the first attempt to apply the formulae of multiple regression to the problem of heredity. It endeavours to show how Galton's correlations must be brought into touch with his "contributions."

The paper is now inadequate because : (i) we now know much better values of the ancestral correlations—we had then only very few data ; and (ii) there are one or two bad algebraical slips.

These are corrected in

K. Pearson : *The Law of Ancestral Heredity*, *Biometrika*, Vol. II. p. 211.

But another stupid blunder is made in this paper on p. 224; where by an oversight *a* and *r* are given the individual and not the mid-parental values. I hope this has been finally put right in this note.

Galton contributed a paper, *R. Soc. Proc.* Vol. 61, p. 402, on the Ancestral Law in Basset Hounds, but this is really written from a somewhat different standpoint ; that standpoint has been considered by me in a paper on the *Law of Reversion*, *R. Soc. Proc.* Vol. 66, p. 140.

There has been a great deal of perfectly idle criticism of the Law of Ancestral Heredity (Archdall Reid, Bateson, Darbishire) principally based on a crude application of Galton's original $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, ... contributions to individuals with *selected* ancestry (Darbishire, Castle, etc.). The least that can be said of these criticisms is that the writers had not grasped the fundamental idea of correlation before they started to criticise the ancestral law.