Heritability in populations and pure lines.

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May 9, 2020

Abstract

A translation of the conclusion of Johannsen's monograph regarding heritability in pure lines. Originally published 1903 by G. Fischer in Jena as Erblichkeit in Populationen und in reinen Linien*.*

I. Translator's note

*This translation currently includes pp. 57-68 of Johannsen's monograph, beginning with the chapter heading "*Zusammenfassung und Rueckblick*". This is the fifth of five chapters. The previous chapters consist of an introduction and three chapters describing "*Untersuchungsreihen*", independent groupings of experiments on quantitative traits of beans (first two* Untersuchungsreihen*) and barley (third* Untersuchungsreihe*).*

Throughout I have occasionally included footnotes drawing attention to pertinent sections; these are in italic and prefixed with MOP *to distinguish them from Johannsen's own notes.*

II. Summary and Review

Everything dealt with here yields at the same time a complete confirmation and a complete resolution of the well-known reversion law of Galton, concerning the behavior between parent and offspring. Other regression behaviors are not relevant to this discussion.

Specifically, so far as my research material allows, it agrees with Galton's teaching that individuals deviating from the average character of the population give descendants that–on average–deviate to a lesser extent in the same direction. A selection in the population therefore effects greater or lesser shifts–in the direction of selection–of these same average characters for which individuals in the population show fluctuating variation.

However, I do not maintain a position viewing populations as units; rather, my material of "pure lines" can unravel these units. In all cases the reversion inside pure lines is shown to be effectively complete: **selection inside pure lines has brought forth no shift of the type.**[1]

The shift of the average character by selection, which can usually be brought about in populations, is therefore dependent–at least in my material–upon the composition of the given populations out of different lines. These types can be more or less different from one another: ordinary selection in populations is performed in an impure fashion, and the result depends on imperfect isolation of the component lines, whose types deviate from the average character

*translation by Maximilian Oliver Press 2020

[1] *MOP: my emphasis*

of the population.

The ordinary and familiar selection result is successive steps in the direction of selection over the course of generations, which depends therefore on the progressive purification of these deviating lines with each generation. It will be easy to see that the action of selection cannot lead across certain boundaries–rather, it must cease when this purification, practically speaking the isolation of the most strongly deviating lines, is fully carried out. In this context it must be added that one cannot be certain from the agreement of a table of variations or curve with the behavior of the exponential error law (the binomial form) that one achieve only a single type in the variant material. The variation curves of individuals of a racially pure (in the ordinary sense) population may frequently, or perhaps even in most cases, express themselves as if composed of numerous types in the form of different lines in the population. The average value therefore has absolutely no correspondence to a true type. In this fashion the impoverishment of a purely statistical method is made obvious.

I have therefore strived throughout this work to distinguish sharply between the concept of the average (average character, average value, etc.) and the concept of a type itself[2]. The confusion of these two very different ideas has led to frequent misunderstandings and erroneous conclusions, and not only in the study of heritability. It must however be conceded that in certain cases closer analysis can be quite difficult; and in pure lines very frequently the two conceptions have the same content. The measurable expression of a type is thus very frequently, if by no means always, an average.

For morphological characters–or at least for groups of them, whose worth for systematic relationships is just becoming generally recognized–the difference between different types is such that, in spite of all variation, single individuals can mostly be placed, with no greater uncertainty than to one or to the other of the closest systematic groups (for example the "small types" of Jordan).

Most morphological types can hardly be arranged in an even succession of variation, such that a mixture of individuals from different types can be confused with a series of individuals belonging to a single type. A mixture of De Vries' Oenothera forms (or of Raunkiaer's Taraxacum "sexes"[3]) gives a rather different picture for a morphological character than a pure culture of a single form.

For all manner of more physiological characters things stand rather differently–for example the non-botanical characters of Hj. Nilsson–as for most quantities of size or other measurements, chemical qualities, specific numerical relations and others. Here the different types show only quantitative differences, even though their differences are factual and easily provable through isolated growth. This means that the variation curves of different types can flow together, and one has then the transgressive curves of De Vries. A mixture of individuals belonging to well-defined different types with respect to one such character (small and large, or narrow and broad beans) may therefore very easily yield an even series of variants such that type differences are not directly easy to know, while one may mistakenly take the average value of the mixture as if it were a single type. In these cases it is impossible to assign types at the level of single individuals. Table 3 (original page 34) gives a very good example for illustration.

Out of these more or less clearly known or felt causes, the study of the former (I would like to say "true") morphological characters has been the focus of systematics. Now in later times the more physiological characters are brought into the sphere of interest of systematics, especially so for the lower forms. It is in these relations particularly that the mutationist

[2]see note 2 on original page 4.

[3]C. Raunkiaer, Kimdannelse uden Befrugtning hos Maelkebotte (Botan. Tidsskrift, Vol. XXV, Copenhagen 1903, p. 109-130.

perspective has its present best support, for the really morphological characters. On the other hand these characters, which principally speak to the entire habitus of the plant, cannot (or can only partially) be expressed numerically, and their appreciation is therefore nearly always outside the realm of the exact methods of measurement and calculation.

The biometrical characters, namely the exact investigation of the laws of variation and heritability, can therefore be clearly expressed in number, measure or weight, unlike the more physiological characters or the Batesian meristic characters. And here, where type differences will decide the comparison between individuals and individuals are even not from manifestations of the fluctuating variability, the Galton-Pearson conception has its fastest stronghold: here one must without consideration of the pure lines necessarily come to the result that the selection of deviating individuals effects (plus or minus variants) a real shift of the type. It is apparently these completely warranted conceptions that the biometricians (as represented by Weldon and Pearson) must frustrate that take mutations as something different and more important than fluctuating variation. And with the present statistical experiences regarding heritability in populations, the consideration of mutations will maybe not be necessary for biology. I say here "maybe" in order to bring myself somewhat closer to the biometricians. For me the polished investigations of Hugo de Vries have long since distanced us from doubt regarding the existence of mutations.

After my results presented here it will appear that the foundation of the Galton-Pearson laws, the relation between parent and offspring, is somewhat different than was previously taken as given. The personal qualities of the parents, grandparents or any ancestors has–so far as my experience indicates–no influence on the average character of the offspring. It is rather the type of the line, which defines the average character of the individual, obviously in intimate collaboration with the influence of the outer life history of the location and time. (The "line" is so far "completely constant and highly variable", as De Vries has so distinctively and apparently paradoxically expressed a similar behavior.[4])

By that it should not be implied that pure lines should be absolutely constant.

First, it is possible that a selection of fluctuating variants over very many generations can shift the type of a line. Nothing positive speaks for this–the data of the biometricians relate to populations, as is often said. These are not decomposed into pure lines and likely cannot be so decomposed. The full evidence of time will demonstrate which means such selection will favor.

Second, we have to consider crosses–thereby the lines will no longer be pure! However, the entire question of bastardy does not lie under discussion.

Third, however, mutations are possible jerky alterations of types. To explain this as such would be highly premature, as their existence must be demonstrated in a much broader scope than it has up until now. That they occur is to me without doubt; I hope in later work to be able to share my own positive results. For now, all that can be said is that a mutation in a given direction cannot be especially expected in the offspring of individuals that deviate in that direction.

To this point I must indicate some delicate questions, which are in the work of De Vries, that one occasionally first observes minus variants of the newly appeared types–a thing that has quite rightly awakened the skepticism of the biometricians. Hopefully continuing studies will bring clarity regarding these observations, which only apparently blur the boundary between fluctuating variability and mutation.

(In supplement: in the final volume of his "Mutation Theory"–in which this work appears in the second edition–De Vries (*loc. cit.* pp.503-504), motivated perhaps by genius, observed

[4] *The Mutation Theory*, Volume I, p. 97.

how in most cases mutations first appear in hybrid forms. Therein lies an extremely important point towards the explanation of the behaviors observed here.)

Hugo De Vries has in his mutation theory (Volume I, p. 368 ff.) a special chapter regarding "nourishment and natural selection", in which he discusses particularly the later effects of rich or sparing nourishment of a mother plant. I do not doubt that different observations have been made, which may be actual or putative, related to the operation or irrelevance of selection, which can find their explanation in this above-mentioned point of De Vries. And of particular interest is the phase of ontogeny called the "sensible period" by this same researcher. In my material presented here I have barely made any contact with these ideas. Obviously it is not my opinion that the "Principle of Pure Lines", without any further considerations, will explain all the forms of character shifts which may arise from selection in combination with extreme or special conditions of life. In this direction, which is deeply interesting to Neo-Lamarckism, there is yet very much to investigate–and to be sure, actual pure lines are a starting point for this.

My goal here was only to illuminate Galton's principle of regression between parents and children, and here I believe that my material, like Galton's, quite evidently has a completely natural character, and its worth is that it forms a basis for the analysis of Galton's laws given for population. My data bring together Galton's results with the ideas of De Vries.

If my experiments are correct, and their scope reaches beyond merely a few special cases, then the general results of this work form a not-insignificant support for the present teaching (represented especially by Bateson and De Vries) of the great importance of "discontinuous" variations or "mutations" for the study of descent. Namely, because a selection in populations operates in my cases only in so far as it contains representatives of already-existing types. These types are not successively developed, for example through protection of those individuals which exhibit fluctuating variation in a particular direction; they are rather found and isolated.

For the study of heritability in populations, pure lines sometimes may not be isolated because of steady necessary cross-fertilization or crossing. Notwithstanding, experience must serve as a basis, by which the study of pure lines may be obtained–here however it must be combined with learning from the study of hybrids. However, closely inspected, this result stands in full agreement with the basic thoughts in the great, often-named work of De Vries–as one see, my end of the results is reached through a different way from that which he follows. Yet further, and most importantly, they support each other through different sorts of facts.

I would regret it to the highest degree if the reader has received the impression that the worth of the significant works of Galton, Pearson, and further biometrical researchers is cast into doubt. The treatment especially from Pearson regarding questions of ancestral influences in some given population I would not dare to criticize. I believe rather that the principle of pure lines in the hand of a Pearson would drive biometrical study much further than the study of populations. Obviously, the relations studies by Pearson have their great scientific meaning and they have immense practical interest. However, they do not suit themselves to casting light on the fundamental laws of heredity.

And concerning especially the researches of Galton, I see nothing in these results that does not confirmation the basic thoughts of Galton's "stirp" teachings, already conducted in 1876.[5] These teachings contain essentially all of the actual value of Weismann's later theories regarding the "continuity of the germplasm". Weissmann's speculations[6] are more plainly presented, but for all that they cannot outrun Galton's in genius and original ideas, and are partially reliant upon them. Galton himself in his later publications on stirps has rather specifically been incorporated well into advancing research. The idea of stirps does not agree well with the regression laws of Galton–however they could hardly be better supported or illustrated than through the results I have presented here. First, the average complete regression to type of lines appears to me the most beautiful evidence for the rightness of Galton's stirp teachings. All things considered, the stirp teachings of Galton are retained unchanged. While Weismann in past times represented (much like Galton) the organs their respective cell precincts through "determinants"–or however one would prefer to name these theoretical corpuscles of heritability–De Vries has done the great service of representing the characteristics (single characteristics) as a whole "pangene"–a publication which dates to 1889[7] and is further motivated in the "The Mutation Theory". It seems to me that the Galton-De Vries theory is overall the only one necessary–and really quite necessary–theory of heritability.

Should the foregoing work succeed to establish pure lines as an unavoidably necessary principle for the actually advanced research in the area of heritability research, the main motivation of this work would be fulfilled. Later publications will further illuminate the behavior of lines which vary in a multimodal or polymodal fashion, while presently only unimodally varying lines have been considered[8]–rather first I represent the simplest cases in my report.

The chain of reasoning that finishes these researches is in its simplicity well-expressed with the oft-cited words of Goethe:

"Dich im Unendlichen zu finden
Musst unterscheiden und dann verbinden."

trans.
To find yourself in infinity
You must divide and then conjoin.

Vilmorin expressed the distinction, Galton taught us the regular connections; what I attempted here is to connect the points that are in honor owed to the genius of these two workers.

At the conclusion of this work, which I presented February 6 1903 to the Danish Society of Sciences[9], I must express my warmest thanks to my true collaborators, especially the gentlemen Dr. phil. Kölpin-Ravn, Mag. scient. A. Didrichsen and cand. hort. H. Stenboek. And without the special financial support of the Carlsbergfonds and the Royal Danish Agricultural College it would have been impossible to carry out the experiments whose first results lie before you.

[5] I am familiar with Galton's teachings from his original essay in Revue scientifique Tome X, 1876, p. 198 (Theorie de l'hérédité).

[6] The position of the biometricians towards "Weismannism" can be clearly seen through Pearson's essay in this direction "Socialism and natural selection" (Fortnightly Review July 1894. Printed in Pearson's Chances of Death, Volume 1, 1897, p. 104). I have here abstained from going further into these questions.

[7] De Vries, Intracellulare Pangenesis, Jena 1889.

[8] De Vries has dealt in "The Mutation Theory" (Volume II, p. 509) with a special case of heritability in a pure "bimodal" line from my correspondence.

[9]