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Remarks on Professor Lloyd's Note on Inheritance of Fertility

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know that a few rabbits can stock a continent with their kind. May not, therefore, all the *Nesokias* be derived from an original pair or two which were in the first case the offspring of *Gunomys*?

The supposition that every species was derived from a single pair is so ancient as to appear ridiculous, but the scientist can only say that there is no evidence in favour of it. But is there no evidence in favour of it? If it can be shown that there are in the world groups of animals of very limited numerical strength (less than a hundred) each member of which possesses certain special characters uniting it with its group fellows and separating it from all other animals, the demonstration will in my opinion afford evidence in favour of this supposition. I have shown elsewhere* that such groups not only exist, but are common, at least among the rats of India. In order to obtain knowledge of these groups it is necessary to examine animals in very large numbers and over wide areas. At the present day such groups are overlooked because it is the custom of naturalists to search for new species. A new species is in itself considered to be an interesting thing. A type specimen is chosen as a representative of the species and the supposition is thereby made that this type specimen is one of an unknown but large number of like animals. But the numerical strength of the "species" is never enquired into, it may not be large, it may be ten, fifty or a hundred.

A new species may be confined to a single house or to the corner of a field or even to a single nest. Rare species are indeed plentiful. It may be asked—"What has all this to do with the question of fertility?" I will endeavour to show the connection. A small group can only become a large one when production is in excess of elimination. A new group will grow up among an old group either because its new features are of life-saving value to it and tend to reduce elimination, or because the new group has a higher rate of production than the old one. Since the distinguishing marks of species do not as a rule appear to be of life-saving value to their possessors, I conclude that in many cases the new groups must grow in numbers simply because they have a higher rate of production, but this conclusion is untenable if we are to hold with Professor Pearson that differences of fertility are never inherited.

VII. Remarks on Professor Lloyd's Note on Inheritance of Fertility.

By KARL PEARSON, F.R.S.

Professor Lloyd says that no new principle was deduced by him from his observations, and again that he "propounded no principle bearing on Evolution or any other subject." Either he has overlooked what he himself wrote, or else he must have very vague ideas of what does bear on Evolution. Yet he wrote p. 262 of his memoir: "The result obtained was quite unexpected [presumably therefore it was *new*]. The maximum fertility of rats (as measured by the number of young which they produce at a birth) is not one with the character which is the type as regards size. In other words, gigantic and dwarfed rats are just as fertile as common rats of average size."

Thus Professor Lloyd himself says that as far as size was concerned there was no "maximum fertility." Professor Lloyd used this result to combat the principle that, if there were a maximum fertility, it must be associated with the modal value of the character, or the race could not be stable. How where there was in his opinion no maximum fertility observable in his experiments, he could use its non-existence to combat a statement of where it would occur, if it existed, I fail to understand.

He further states that he laid no stress on this (B) absence of differential fertility in rats, and that he did lay stress on (A) the maximum fertility of rats not being associated with the type as far as size is concerned. As he had, according to his own interpretation of his

* *Records Indian Museum*, Vol. III. Pt. I. and Vol. V. Pt. II.

observations, shown that there was no maximum fertility at all, it is hard to comprehend what value he set on his observations. Apparently, he desired to show that a maximum fertility could exist not associated with the type character. That I take it would be a new principle, and one which I should have said would have an enormous bearing on Evolution. As a matter of fact in the "Conclusions" given in his memoir (p. 264), there is no reference to (A), but the result (B) he emphasises by *italics*.

"There is clear evidence that the largest and smallest rats are quite as fertile as those of average size" (p. 264). As there was "clear" evidence of the exact opposite of this statement in his observations, and as the age and number of litters of his rats were not given, it was quite impossible to determine from Captain Lloyd's data, whether (i) there was any maximum fertility at all associated with size and (ii) if there were, with what size it was associated.

Professor Lloyd drew the very definite conclusion that fertility was not related to weight in his rats; Fraülein Hanel drew the very definite conclusion that there was no inheritance within the "pure line" in her *Hydra*. Both of these conclusions were erroneous, as the most elementary statistical examination would have shown either of them. I used both to illustrate the point thrust on me daily by the examination of many memoirs that biology cannot safely do without biometry. Professor Lloyd states that some principle enunciated by me is "now occupying a prominent position in a well-known text-book." I cannot be responsible for that text-book, whichever it may be, nor how the principle may be stated. The essential contributions I have made to this supposed principle may be summed up as follows.

(i) Genetic selection, i.e. fertility correlated with a somatic character will modify natural selection, unless the modal somatic character exhibits the maximum fertility. A progressive change in type would follow any other association until the modal value became that of maximum fertility. (*Phil. Trans.* Vol. 187, A, 1896, p. 258; Vol. 192, A, 1899, p. 258, etc.)

I cannot see any flaw in this argument whatever.

(ii) Genetic selection either does not exist or if it does there is instability in the race.

In the *Grammar of Science* (2nd Edition, 1900, p. 440 *et seq.*) I referred to two species of flowers in which I had found the modal capsules to contain the greatest bulk of fertile seed. If I had found non-modal capsules to contain such bulk of fertile seed, I should, having shewn that the character I was dealing with was inherited, have argued that the plant in question was changing or could change its type independently of natural selection, i.e. that genetic selection would at least modify if it did not overmaster natural selection. If Professor Lloyd had been right in asserting that there was no relation between fertility and weight in his rats then there could be no genetic selection, and what he calls my principle could not come into play. For the basis of that principle lies in the words: "If fertility be correlated with any organ or character." Actually Professor Lloyd's data showed a considerable correlation between weight and size of litter; and if this had been correct then genetic selection would have come into play and he would have reached an important result—just the reverse of what he himself drew from his own statistics!—As a matter of fact, I think his material was vitiated because he had not inquired into the age factor and the correlation of age and size of litter in his rats. There was nothing in his material which would demonstrate or refute the principle that when fertility-differentiation exists and is correlated with somatic character, then the modal character must be associated with the maximum fertility, or the race will lack stability in type, until this association is attained. Professor Lloyd remarks:

"The conclusion that there is a strong tendency for the character of maximum fertility to become one with the character which is the type is in my opinion unjustifiable in any case, because it seems that an individual cannot represent the type of its race as regards all its features. We can only speak of a typical individual when we are dealing with one measurable feature at a time."

I don't think I ever read a passage which shows greater need for biometric training in a biologist! Can Professor Lloyd have the least conception of what are the leading features of a multiple frequency surface? Has he never heard of the "mean man" of Quetelet, or of Edgeworth's defence of that "mean man's" actuality? The uniqueness of the mode in most multiple frequency surfaces is a well-established fact, and if Professor Lloyd will strive to see what follows a differential fertility correlated with a non-modal somatic character, he will quickly discover how few generations suffice to make that somatic character the modal value.

Professor Lloyd asserted on the basis of his rats that there was no relation of fertility to weight, he now says that I agree with him that there was no relation of modal weight to fertility. I regret that I do nothing of the kind. Knowing that age is related to weight and to size of litter I am quite unable to assert that his data prove or disprove anything at all with regard to fertility. I am only in a position to say that I have not, hitherto, been able to find a *marked* inheritance of fertility *within the race*, and begin to doubt its existence*. Professor Lloyd now turns round and leaves the question of fertility within the race which he had been discussing and to which his data applied, and says that in two races, which he himself differentiates by the *number of teats* with which they are provided, one has a greater fertility than the other. That is to say he passes from an intraracial to an interracial problem and from weight of rat to number of teats without apparently noticing the jump. Fertility pure and simple may be correlated with many things. Net fertility in man is correlated with the size of the pelvis, but because the pelvis is a character transmitted by heredity, it does not follow that fertility pure and simple is an hereditary character. The slight intensity of the inheritance of fertility such as we find intraracially in man and other mammals is quite compatible with its being only indirectly transferred because it is correlated with directly inherited characters. If Professor Lloyd wishes to meet my point, he should correlate fertility intraracially with the number of teats and then investigate whether this correlation is zero, or whether the modal number of teats is associated with the maximum fertility. If neither of these things be true, then I am quite sure that he will discover that his race is unstable and rapidly changing its type as far as teats are concerned. But a simple statement that two races of rats have different type fertilities does not seem to me to have any application to what he calls my "principle"—the less so when he tells us that their modal number of teats differ significantly. The appearance of additional teats may be the character, or one of the characters, which may lead to increased size of litter, but this has nothing to do with the intraracial inheritance of fertility pure and simple. It surely confirms my point that instability follows association of fertility with a non-modal character.

* Many investigations have shown some inheritance of fertility: see for example my own paper with Alice Lee and Bramley Moore of 1899 (*Phil. Trans.*, Vol. 192, pp. 257—330) on fertility in man and in the thoroughbred race horse. But later work by others on man, mice, swine, poultry, etc. seems to me to indicate that fertility is not directly inherited, but only to a secondary degree as being correlated with inherited physical characters. The sort of values one finds for the heredity of fertility range from .05 to .15. I think that in 1899 I laid too much stress on the possibility of the *direct* inheritance of fertility, but this was an inference formed before I had determined the high parental correlation of 0.5 for physical characters. I thought then that disturbing factors might possibly reduce Galton's value of $\frac{1}{2}$ for the parental correlation to the low values we had found in the case of man and horse. I do not think they could reduce $\frac{1}{2}$ to those values.