

School of Economics and Political Science, to which he was appointed in 1903, retains the readership in geography, to which, under its then title, he was appointed in 1902.

DISCUSSION AND CORRESPONDENCE

MENDELIAN PROPORTIONS IN A MIXED POPULATION

TO THE EDITOR OF SCIENCE: I am reluctant to intrude in a discussion concerning matters of which I have no expert knowledge, and I should have expected the very simple point which I wish to make to have been familiar to biologists. However, some remarks of Mr. Udny Yule, to which Mr. R. C. Punnett has called my attention, suggest that it may still be worth making.

In the *Proceedings of the Royal Society of Medicine* (Vol. I., p. 165) Mr. Yule is reported to have suggested, as a criticism of the Mendelian position, that if brachydactyly is dominant "in the course of time one would expect, in the absence of counteracting factors, to get three brachydactylous persons to one normal."

It is not difficult to prove, however, that such an expectation would be quite groundless. Suppose that Aa is a pair of Mendelian characters, A being dominant, and that in any given generation the numbers of pure dominants (AA), heterozygotes (Aa), and pure recessives (aa) are as $p:2q:r$. Finally, suppose that the numbers are fairly large, so that the mating may be regarded as random, that the sexes are evenly distributed among the three varieties, and that all are equally fertile. A little mathematics of the multiplication-table type is enough to show that in the next generation the numbers will be as

$$(p+q)^2:2(p+q)(q+r):(q+r)^2,$$

or as $p_1:2q_1:r_1$, say.

The interesting question is—in what circumstances will this distribution be the same as that in the generation before? It is easy to see that the condition for this is $q^2=pr$. And since $q_1^2=p_1r_1$, whatever the values of p , q and r may be, the distribution will in any case continue unchanged after the second generation.

Suppose, to take a definite instance, that A is brachydactyly, and that we start from a population of pure brachydactylous and pure normal persons, say in the ratio of 1:10,000. Then $p=1$, $q=0$, $r=10,000$ and $p_1=1$, $q_1=10,000$, $r_1=100,000,000$. If brachydactyly is dominant, the proportion of brachydactylous persons in the second generation is 20,001:100,020,001, or practically 2:10,000, twice that in the first generation; and this proportion will afterwards have no tendency whatever to increase. If, on the other hand, brachydactyly were recessive, the proportion in the second generation would be 1:100,020,001, or practically 1:100,000,000, and this proportion would afterwards have no tendency to decrease.

In a word, there is not the slightest foundation for the idea that a dominant character should show a tendency to spread over a whole population, or that a recessive should tend to die out.

I ought perhaps to add a few words on the effect of the small deviations from the theoretical proportions which will, of course, occur in every generation. Such a distribution as $p_1:2q_1:r_1$, which satisfies the condition $q_1^2=p_1r_1$, we may call a *stable* distribution. In actual fact we shall obtain in the second generation not $p_1:2q_1:r_1$ but a slightly different distribution $p'_1:2q'_1:r'_1$, which is not "stable." This should, according to theory, give us in the third generation a "stable" distribution $p_2:2q_2:r_2$, also differing slightly from $p_1:2q_1:r_1$; and so on. The sense in which the distribution $p_1:2q_1:r_1$ is "stable" is this, that if we allow for the effect of casual deviations in any subsequent generation, we should, according to theory, obtain at the next generation a new "stable" distribution differing but slightly from the original distribution.

I have, of course, considered only the very simplest hypotheses possible. Hypotheses other than that of purely random mating will give different results, and, of course, if, as appears to be the case sometimes, the character is not independent of that of sex, or

has an influence on fertility, the whole question may be greatly complicated. But such complications seem to be irrelevant to the simple issue raised by Mr. Yule's remarks.

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P. S. I understand from Mr. Punnett that he has submitted the substance of what I have said above to Mr. Yule, and that the latter would accept it as a satisfactory answer to the difficulty that he raised. The "stability" of the particular ratio 1:2:1 is recognized by Professor Karl Pearson (*Phil. Trans. Roy. Soc. (A)*, vol. 203, p. 60).

PURE CULTURES FOR LEGUME INOCULATION

In the 1907 Report of the Biologist of the North Carolina Agricultural Experiment Station, Dr. F. L. Stevens and Mr. J. C. Temple report some work upon cultures of the nodule-forming organisms of legumes. The cultures used were obtained from the United States Department of Agriculture. The investigators have presented their data in such a manner that the value of pure cultures for inoculating legumes appears questionable and their conclusions emphasize their attitude of disapproval. In carefully reviewing their report, a very brief outline of which appeared in *SCIENCE*, Vol. 26, 1907, p. 311, I have been impressed with the fact that the inferences drawn by the casual reader would almost certainly be unwarrantably antagonistic to the use of pure cultures for inoculating legumes. The investigators' objections to the actions of cultures supplied by this department are briefly as follows:

A considerable number of the cultures hermetically sealed in glass were sterile at the time they were examined by Dr. Stevens and Mr. Temple. The misconception in regard to the viability of cultures distributed by the department at the present time could have been prevented by the insertion of a footnote explaining that since July, 1906, small bottles with wax seals have been substituted for small tubes hermetically sealed in the flame of a blast lamp. It is surprising to

me that four out of seven of the old-style cultures examined by Dr. Stevens should have been sterile, as my own investigations previous to adopting this method for distribution indicated that about one half of one per cent. of the cultures sealed in this way in routine work would be injured or sterilized by the heat of sealing. The law of chance must perhaps be invoked to explain the discrepancy in our figures. It must be remembered, however, that the cultures spoken of at this time are the old-style liquid cultures, and that the cultures distributed since July, 1906, are not open to criticism of this sort.

It is surprising to me also to learn that during the multiplication period conducted in the practical manner outlined for use on the farm such great contamination should have become manifest. Two years ago I had small samples of these gross cultures prepared on the farm returned to me by farmers in various parts of the country for examination, the sample being taken and mailed to me at the time the culture was applied to the seed. This, of course, allowed for greater development of contaminations than would have taken place at the time the culture was applied to the seed. Even with this handicap about two per cent. of the cultures received from the farmers were apparently pure, and if contaminated the contamination was evidently very slight indeed. About sixty per cent. were contaminated, but not excessively so, it being easy in all of these cases to isolate large numbers of *Pseudomonas radicola*. The remainder were in rather bad condition, although I doubt if ten per cent. of the entire number received were so seriously contaminated as to be worthless.

The description of the pot experiments conducted by Dr. Stevens and Mr. Temple is confusing. In the first place, the sterilizing of soil by heating is well known to injure the soil seriously, and, regardless of the condition of the nodule-forming bacteria introduced, it is an open question whether soil sterilized by heating would allow nodule formation until a normal bacteriologic flora and normal soil conditions generally had been reestablished. It is impossible to determine whether any

retary of the Pan American Institute of Mining Engineering and Geology, has been commissioned by the Chilean Government to study fuel technology at the Pennsylvania State College. He plans to spend ten months in studying methods of reducing coal to liquid fuel and metallurgical coke.

By unanimous vote of the council of the American Association of Pathologists and Bacteriologists, the annual meeting planned for April 1 and 2, at the University of Chicago, has been cancelled. According to a statement issued by Dr. Howard T. Karsner, *secretary*, this action was determined by the great pressure of work due to depleted staffs, the presence of many members in the military service, limitations on transportation, doubt concerning hotel accommodations and the probability that any program that might have been arranged would not be comprehensive. The authorities of the University of Chicago were willing to proceed with arrangements, but the council deemed cancellation patriotic and wise. The council will meet early in April to transact necessary business. Nominations for membership, together with supporting data and not less than two letters of recommendation, should be in the office of the secretary not later than April 1.

AN Associated Press dispatch dated January 27 reports that a joint resolution requesting President Roosevelt to issue a proclamation designating February 11 as Thomas Alva Edison Day has been introduced in the House by Representative Frank L.

Sundstrom of New Jersey. Mr. Sundstrom stated that the celebration of Mr. Edison's birthday this year was being directed toward helping to increase war production.

It is reported in the *Journal* of the American Medical Association that essays for the Lucien Howe Prize of the Medical Society of the State of New York must be received by the chairman of the committee on prize essays, Dr. Charles G. Heyd, 292 Madison Avenue, New York, not later than March 1. One hundred dollars will be presented for the best original contribution on some branch of surgery, preferably ophthalmology, during the annual meeting of the medical society in Buffalo in May.

By the will of Mrs. Anna Burr, the bulk of her estate of the value of \$2,000,000 is bequeathed to the Lankenau Hospital of Philadelphia in memory of her husband, the late Edward H. Burr, one of the chief owners of the old Link-Belt Company. The fund will be used for cancer research.

The Biological Bulletin is publishing, as a separately bound supplement to its February issue, a serial list of all the holdings of the Marine Biological Laboratory Library. It covers approximately eighty pages, and lists with cross references the 2,259 titles of journals in the library. Titles are listed alphabetically to conform to the arrangement of the stacks in the library, and hence should serve as a guide book to the library itself as well as an aid in securing microfilm copies of articles.

DISCUSSION

THE HARDY-WEINBERG LAW

ONE of the basic relations in the genetics of populations is expressed by the statement that in a very large random-mating population in which two alleles A and A' occur in the frequencies p and q ($= 1 - p$) the three types AA, AA' and A'A are expected to remain in equilibrium from generation to generation at frequencies of p^2 , $2pq$ and q^2 , in the absence of mutation or selection. This theorem, of which a special case was discovered by Pearson (1904), is known in its general formulation as Hardy's law, or Hardy's formula (*e.g.*, Sinnott and Dunn, 1939, Sturtevant and Beadle, 1939, and Dobzhansky, 1941). It is the purpose of this note to point out that the important population formula was independently and simultaneously recognized by the Stuttgart physician, Wilhelm Weinberg (1862-1937). On January 13, 1908, Weinberg gave a lecture before the "Verein für vaterländische Naturkunde in Württemberg" under the title "Über den Nachweis der Vererbung beim Menschen."

In the course of a keen exposition of both the difficulties to be met by students of human heredity and of statistical approaches which should help to overcome these difficulties, he derived the equilibrium law. The full lecture was printed in the *Jahreshefte* of the Verein, Volume 64: 368-382 (1908), and appeared sometime before the fall of 1908 as judged by the stamped entry on the title page of the volume which I have consulted: "Academy of Natural Sciences of Philadelphia, Sept. 28, 1908." Hardy's note in *SCIENCE* is signed April 5, 1908, and is published in the July 10, 1908, number.

The following is a translation of the relevant section of Weinberg's communication making corrections for three minor typographical errors:

Quite different is the situation when one considers Mendelian inheritance under the influence of panmixis. I start from the general premise that there are originally present m each of pure male and female representatives of type A and correspondingly n of each pure repre-

sentatives of type B. If these cross at random one obtains, by applying the symbolism of the binomial theorem, the following composition of the filial generation:

$$\frac{(mAA + nBB)^2}{(m+n)^2} = \frac{m^2}{(m+n)^2} AA + \frac{2mn}{(m+n)^2} AB + \frac{n^2}{(m+n)^2} BB$$

or if $m+n=1$

$$m^2 AA + 2mn AB + n^2 BB.$$

If now the male and female members of the first generation are crossed at random among themselves one obtains the following frequencies of the various cross combinations:

$$m^2 \cdot m^2 \cdot (AA \times AA) = m^4 AA$$

$$4m^2 mn (AA \times AB) = 2m^3n AA + 2m^2n AB$$

$$2m^2n^2 (AA \times BB) = 2m^2n^2 AB$$

$$4(mn)^2 (AB \times AB) = m^2n^2 AA + 2m^2n^2 AB + m^2n^2 BB$$

$$4mn n^2 (AB \times BB) = 2m n^3 AB + 2m n^3 BB$$

$$n^2n^2 (BB \times BB) = n^4 BB$$

or the relative frequencies

$$AA : m^2 (m+n)^2$$

$$AB : 2mn (m+n)^2$$

$$BB : n^2 (m+n)^2$$

and the composition of the second filial generation is again

$$m^2 AA + 2mn AB + n^2 BB.$$

Thus we obtain under the influence of panmixis in each generation the same proportion of pure and hybrid types. . . .

While Weinberg's paper, like Mendel's, appeared in an obscure journal, its failure to be recognized can not be ascribed to this fact alone. His later contributions dealing with extensions of the statistical treatment of the genetics of populations are found in the "regular" journals. These papers have received some attention (*e.g.*, Sewall Wright, 1930) and in them Weinberg refers to his 1908 pioneer work. However, both Weinberg and Hardy were ahead of contemporary thought and similar problems were not generally considered for at least eight years. At that time perhaps Hardy's name and the prominent place of his publication both helped to leave Weinberg's contribution neglected.

Hardy as a mathematician did not follow up his discovery by any further consideration of its genetic implications. Weinberg in 1909 reformulated his theorem in terms valid for multiple alleles—at a time when no case of multiple alleles had been discovered in man nor in plants and even Cuénot's demonstration of multiple alleles in the mouse had remained unnoticed. He also for the first time investigated polyhybrid populations and recognized their essentially different method of attaining equilibrium. Considering these facts it seems a matter of justice to attach the names of both the discoverers to the population formula.

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THE SHOT-PUT AND THE EARTH'S ROTATION

IN SCIENCE for August 28, 1942, Joseph O. Thompson cites with skepticism a recently published statement¹ to the effect that the earth's rotation enables an athlete to put the 16-pound shot farther toward the east than toward the west. As a matter of fact there was nothing new about the statement. Artillerists in all the world's armies have been aware of the very definite effect of terrestrial rotation upon the ranges of projectiles for generations and have corrected the aim of long-range guns accordingly as a matter of regular routine.

The effects upon the ranges of athletic projectiles are not large but they are definitely larger than the precision of measurement which is implied when a hammer throw is recorded in the record book as, for example, 176 ft. 11½ in. or a shot-put as 52 ft. 6 3/16 in. These effects have nothing to do with the drag of the air and are in addition to any consequences deriving from the fact that gravity itself depends partly upon the centrifugal forces of our rotational motion. They are due rather to the fact that the gravitational pull upon the projectile is applied in a constantly changing direction as the earth turns, and to the further fact that the landing surface does not await the arrival of the projectile in the same relative position as it occupied when the firing occurred, but instead drops away from the projectile to the eastward or rises to meet it from the west, thus either extending or curtailing the measured range. Non-mathematical explanations are, of course, incomplete.

A few years ago the writer of this note published an article² upon this and other inaccuracies in the metrology of sport, inaccuracies which have, beyond the slightest doubt, imposed definite and calculable handicaps upon some competitors while favoring others. Reprints of this article were sent to all the several hundred committeemen of the Amateur Athletic Union of the United States in the faint hope that improvements in the handling of the data of field sports might result. One committeeman acknowledged receipt of the reprint but there has been nothing to indicate that any of them read it.

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THE WATER HYACINTH IN CALIFORNIA

THE water hyacinth, *Eichornia crassipes* (Mart.) Solms, which became a serious hindrance to navigation in the streams of Florida, has been known from a few isolated localities in California for a good many years. In 1922 Jepson¹ reported it as occurring at

¹ *Collier's*, July 4, 1942, page 6.

² *Scientific American*, April, 1937.

¹ W. L. Jepson, *A Flora of California*, 1: pt. 6, 247, 1922.