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G.H. Hardy: Mathematical Biologist

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Synopsis

Godfrey Harold Hardy (1877–1947), the magnificent analyst who "discovered" the enigmatic Ramanujan and penned *A Mathematician's Apology*, is most widely known outside of mathematics for his work in genetics. How did Hardy, described by his colleague C.P. Snow as "the purest of the pure," become one of the founders of modern genetics? We explore this question in light of Hardy's own ideas about pure and elegant mathematics.

Godfrey Harold Hardy (1877-1947), the magnificent analyst who "discovered" the enigmatic Ramanujan and penned *A Mathematician's Apology*, is most widely known outside of mathematics for his work in genetics. Hardy's fame stems from a condescending letter to the editor in *Science* concerning the stability of genotype distributions from one generation to the next (see Figures 1-2). His result is known as the Hardy-Weinberg Law, and every biology student learns it today.

How did Hardy, described by his colleague C.P. Snow as "the purest of the pure" [8], become one of the founders of modern genetics? What would Hardy say if he knew that he had earned scientific immortality for something so mathematically simple?

In a lecture delivered by R.C. Punnett (of Punnett square fame), the statistician Udny Yule raised a question about the behavior of the ratio of dominant to recessive traits over time. This led Punnett to question why a population does not increasingly tend towards the dominant trait. He was confused and brought the question to his colleague, G.H. Hardy, with whom he frequently played cricket (for the complete story, see [2, 3]).

Under certain natural assumptions, Hardy demonstrated that there is an equilibrium at which the ratio of different genotypes remains constant over time (this result was independently obtained by the German physician Wilhelm Weinberg). There is no deep mathematics involved; the derivation of the Hardy-Weinberg Law involves only "mathematics of the multiplication-table type" [6]. Hardy's brief letter dismisses Yule's criticism of Mendelian genetics:

> *"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. . . 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"* [6].

Hardy's letter was short, tinted with contempt, and possibly unnecessary. Geneticist A.E.F. Edwards refers to the affair as "a problem that, if both parties had paid more attention to Mendel's paper itself, should never have arisen" [2]. According to the geneticist J.F. Crow, the Hardy-Weinberg Law "is so self-evident that it hardly needed to be 'discovered' " [1].

This was not an argument that Hardy sought. Punnett reflected that " 'Hardy's Law' owed its genesis to a mutual interest in cricket" [7]. If they had not played cricket together, Punnett probably would not have asked Hardy about the problem in the first place. Hardy certainly would never have developed an interest in it otherwise, for his aversion to applied mathematics was legendary:

> *"[I]s not the position of an ordinary applied mathematician in some ways a little pathetic?. . . 'Imaginary' universes are so much more beautiful than this stupidly constructed 'real' one"* [5, page 135].

Although Titchmarsh tells us that Hardy "attached little weight to it" [9], the ubiquity of the Hardy-Weinberg Law in introductory biology texts indicates the seminal nature of the result. This contradicts Hardy's bold confession:

> *"I have never done anything 'useful.' No discovery of mine has made, or is likely to make, directly or indirectly, for good or ill, the least difference to the amenity of the world... Judged by all practical standards, the value of my mathematical life is nil; and outside mathematics it is trivial anyhow"* [5, page 150].

However, if we scrutinize Hardy's views and personality more closely, we might gain a more nuanced perspective. Hardy did not detest applications entirely; he instead took pride in the uselessness of his work because it freed him from contributing to the terrors of war and violence:

> *"But here I must deal with a misconception. It is sometimes suggested that pure mathematicians glory in the uselessness of their work. If the theory of numbers could be employed for any practical and obviously honorable purpose, if it could be turned directly to the furtherance of human happiness or the relief of human suffering... then surely neither Gauss nor any other mathematician would have been so foolish as to decry or regret such applications. But science works for evil as well as for good (and particularly, of course, in time of war)..."* [5, pages 120-121].

As an avid atheist, Hardy saw God, rather than applied scientists, as his "personal enemy" [9]. In fact, Hardy was the President of the Association of Scientific Workers from 1924-26:

> *"[Hardy] said sarcastically that he was an odd choice, being 'the most unpractical member of the most unpractical profession in the world'. But in the important things he was not so unpractical"* [8].

Hardy tells us that "the noblest ambition is that of leaving behind something of permanent value." "To have produced anything of the slightest permanent interest," he says, "whether it be a copy of verses or a geometrical theorem, is to have done something utterly beyond the powers of the vast majority of men." Mathematics lends itself to this form of immortality: "Archimedes will be remembered when Aeschylus is forgotten, because languages die and mathematical ideas do not."

Hardy applauded "the permanence of mathematical achievement," regardless of its applicability to the outside world. Concerning the theorems of Euclid and Pythagoras, "each is as fresh and significant as when it was discovered—two thousand years have not written a wrinkle on either of them," despite the fact that "neither theorem has the slightest practical importance." Although he lauded the permanence of mathematical achievement, Hardy was an "anti-narcissist" who "could not endure having his photograph taken... He would not have any looking glass in his rooms, not even a shaving mirror." However, he clearly wanted to accomplish something everlasting, for "mathematics was his justification" [8].

G.H. Hardy achieved immortality, although his most famous accomplishment is not within his own exalted field of pure mathematics, nor is it in a field to which he attached any value. Crow conjectures:

> *"It must have embarrassed him that his mathematically most trivial paper is not only far and away his most widely known, but has been of such distastefully practical value. He published this paper not in the obvious place, Nature, but across the Atlantic in Science. Why? It has been said that he didn't want to get embroiled in the bitter argument between the Mendelists and biometricians. I would like to think that he didn't want it to be seen by his mathematician colleagues"* [1].

Further speculation regarding Hardy's choice of venue can be found in [4].

No one can know with certainty how Hardy would react now, over one hundred years later, to the impact his letter in *Science* had. There is more complexity and depth to him than can be gleaned from his writings, not even in combination with accounts from those who knew him. However interesting and revealing details may be (like those Titchmarsh provided in Hardy's obituary—he liked Scandinavia, cats, and detective stories, but not dogs, politicians, or war [9]), they will never provide a complete picture.

Reflecting on his life, Hardy considered it to be a success in terms of the happiness and comfort that he found, but the question remained as to the "triviality" of his life. He resolved it accordingly:

> *"The case for my life... is this: that I have added something to knowledge, and helped others to add more; and that these somethings have a value which differs in degree only, and not in kind, from that of the creations of the great mathematicians, or of any of the other artists, great or small, who have left some kind of memorial behind them"* [5, page 151].

In all great proofs, Hardy asserted that

> *"there is a very high degree of unexpectedness, combined with inevitability and economy. The arguments take so odd and surprising a form; the weapons used seem so childishly simple when compared with the far-reaching results; but there is no escape from the conclusions"* [5, page 113].

Extending the scope of these criteria beyond mathematics, one can argue that the Hardy-Weinberg Law meets these standards.

References

[1] James F. Crow, "Eighty Years Ago: The Beginnings of Population Genetics," *Genetics*, Volume **19** Issue 3 (1988), pages 473–476.

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[4] Colin R. Fletcher, "Postscript To: G.H. Hardy – Applied Mathematician," *Bulletin - Institute of Mathematics and Its Applications*, Volume **16** Issue 11-12 (1980), page 264.

[5] G.H. Hardy, *A Mathematician's Apology* (with a foreword by C.P. Snow), Reprint of the 1967 edition, Cambridge University Press, Cambridge, 1992.

[6] G.H. Hardy, "Mendelian Proportions In A Mixed Population," *Science*, Volume **28** Number 706 (July 10, 1908), pages 49–50.

[7] R.C. Punnett, "Early Days of Genetics," *Heredity*, Volume **4** Issue 1 (1950), pages 1–10.

[8] C.P. Snow, Foreword to *A Mathematician's Apology*, Cambridge University Press, London, 1967.

[9] E.C. Titchmarsh, "Godfrey Harold Hardy. 1877–1947," *Obituary Notices of Fellows of the Royal Society*, Volume **6** Issue 18 (1949), pages 446–461.

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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 that 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

Figure 1: Page 1 of [6], from http://www.jstor.org/stable/1636004, accessed on July 15, 2015. Courtesy of JSTOR Early Journal Content.

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.

G. H. Hardy

Trinity College, Cambridge,
April 5, 1908

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 radicicola*. 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

Figure 2: Page 2 of [6], from http://www.jstor.org/stable/1636004, accessed on July 15, 2015. Courtesy of JSTOR Early Journal Content.