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J. B. S. Haldane, Ernst Mayr and the Beanbag Genetics Dispute

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Abstract. Starting from the early decades of the twentieth century, evolutionary biology began to acquire mathematical overtones. This took place via the development of a set of models in which the Darwinian picture of evolution was shown to be consistent with the laws of heredity discovered by Mendel. The models, which came to be elaborated over the years, define a field of study known as population genetics. Population genetics is generally looked upon as an essential component of modern evolutionary theory. This article deals with a famous dispute between J. B. S. Haldane, one of the founders of population genetics, and Ernst Mayr, a major contributor to the way we understand evolution. The philosophical undercurrents of the dispute remain relevant today. Mayr and Haldane agreed that genetics provided a broad explanatory framework for explaining how evolution took place but differed over the relevance of the mathematical models that sought to underpin that framework. The dispute began with a fundamental issue raised by Mayr in 1959: in terms of understanding evolution, did population genetics contribute anything beyond the obvious? Haldane's response came just before his death in 1964. It contained a spirited defense, not just of population genetics, but also of the motivations that lie behind mathematical modelling in biology. While the difference of opinion persisted and was not glossed over, the two continued to maintain cordial personal relations.

Keywords: population genetics, evolution, evolutionary synthesis, models, mathematical biology

I am an unrepentant ‘beanbag geneticist.’ Non-mathematicians often fail to realise the complexity of behaviour and sometimes the self-regulatory capacity of material systems composed of simple components. (J. B. S. Haldane)¹

The mistake is in thinking that through mathematical formulae, you can arrive at the truth. That’s wrong. (Ernst Mayr)²

Introduction

Three events demarcate the dispute that forms the subject of this article. The first was the discovery by Gregor Mendel in 1866 of the laws of inheritance. The second was the general validation and elaboration of those laws by (among others) Thomas Hunt Morgan and his school. The third ‘event’ variously is known as the Evolutionary Synthesis, the Modern Synthesis or (less frequently) the neo-Darwinian Synthesis (for the sake of uniformity we stick to ‘Evolutionary Synthesis’ in this article). It consisted of a combination of two developments. On the one hand, with the help of Mendel’s rules and statistical principles, a mathematical formulation of evolutionary change was constructed. At the same time, and almost in parallel, a series of detailed studies in palaeontology, systematics and genetics made a convincing case for the claim that the basis of adaptive evolution was natural selection.

Only the barest description can be given here of what the Evolutionary Synthesis involved. Its progress is easily tracked thanks to numerous signposts: landmark books and major articles, published proceedings of scientific meetings, and biographies. The volume edited by Mayr and Provine³ is a goldmine in that it contains perceptive historical analyses, reminiscences by participants and an extensive bibliography. Smocovitis deconstructs the Synthesis and emphasises its

¹ Letter dated 8 May 1963 from J. B. S. Haldane to Ernst Mayr (No. HUGFP 74.7, BOX 9, F 820; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

² Ernst Mayr, interviewed by Michael Shermer and Frank J. Sulloway for “Skeptic” (8 January 2000; see <http://www.skeptic.com/eskeptic/04-07-05>).

³ Mayr and Provine, 1980, 1998.

philosophical bases.⁴ Lasting roughly from the early 1900s through the 1950s, the synthesis was a communal enterprise that involved the unification of a range of disciplines – genetics, systematics, palaeontology, botany and zoology – under the common rubric of Darwinian evolution, meaning, on the whole, natural selection. (Biochemistry, molecular biology, cell biology, developmental biology and ecology do not conform entirely to the rule, because in certain respects they are also engaged in negotiating with various ‘non-Darwinian’ explanatory frameworks. One can view this as a broadening of the Synthesis.⁵) It showed how the laws of Mendel and the facts of organismal evolution could form part of one consistent framework – based largely, though not entirely, on natural selection. Mayr described it as follows⁶:

The term ‘evolutionary synthesis’ was introduced by Julian Huxley in *Evolution: The Modern Synthesis* (1942) to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes (‘mutations’), recombination, and the ordering of the variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms.

The first step in the Synthesis was the recognition that the mechanism of Mendelian (‘particulate’) genetics implied a conservation law: in the absence of any tendency to the contrary (e.g. mutation, migration or selection), heritable variation would be preserved – at least in sufficiently large populations. This supplied a missing element in the theory of natural selection, one that had plagued Darwin, and made it plausible that trait differences between individuals would always remain available for selection to act on. Therefore, *to the extent that* (a) traits were associated with genes and (b) trait differences between individuals were associated with differential survival and reproduction, natural selection was a sufficient explanation for the evolution of traits within populations – and

⁴ Smocovitis, 1992.

⁵ It is commonly assumed that a Darwinian explanation means one based on natural selection. Strictly speaking, this is incorrect. In fact Darwin was “convinced that Natural Selection has been the main but not exclusive means of modification [of species]” (*The Origin of Species*, 1st edition). Still, one imagines that he would have been astonished by the variety of alternatives to natural selection that are seriously discussed today. Our use of ‘non-Darwinian’ refers to explanations involving concepts such as self-organisation and niche construction besides the more familiar neutral theory of molecular evolution.

⁶ Mayr and Provine, 1980 and 1998, p. 1.

perhaps, by extension, as Darwin had hypothesised, accounted for the differences between species and higher groups as well. (The italicised words in the previous sentence set out an operational programme for evolutionary biologists; they imply that evolutionary biology is an empirical science and natural selection is not a tautology.) The apparent discrepancy between a quasi-continuous distribution of morphological traits and the discrete alternatives offered by single gene variation was bridged when it was realised that a single trait could depend on a large number of genes. The Synthesis showed that certain views that had been put forward until then, some of them associated with the name of Lamarck, others with that of Mendel, were untenable: for example directed evolution, whether guided by the environment or ‘inner drive;’ evolution via the inheritance of acquired traits; and evolution through mutations of major effect (saltationism).

The relevant arguments made use of quantitative treatments of genetic change. They led to the setting up of an algorithm for calculating gene (or genotype) frequencies in one generation from their values in the previous generation. In outline, the steps went as follows: Genotype frequencies in zygotes → Genotype frequencies in adults → Gene frequencies in the germ line → Genotype frequencies in zygotes. (Each arrow implies a set of events specified by genetics, physiology, development, behaviour, demography, mating structure, the physical and biological environments, and so on, with the relevant probabilities depending on the underlying genetic makeup.) The mathematical component of the Synthesis – known as population genetics – fuelled the “Beanbag Genetics” dispute. The dispute was initiated during a symposium held 50 years ago to mark the centenary of the publication of *The Origin of Species*. Its chief protagonists were two of the leaders of post-Darwinian evolutionary biology, Ernst Mayr and J. B. S. Haldane.

Aspects of the beanbag genetics dispute have been discussed before. Some authors have focussed on issues pertaining to evolutionary biology, some on history and philosophy.⁷ We touch on these matters only peripherally; the original literature should be consulted for technical details. Our aim is to present a sketch of the dispute as it occurred, in a roughly chronological order. We make use of the beanbag genetics dispute to illustrate several themes. One theme concerns divergent views of the roles of mathematics and model building in biology. A subsidiary theme is the perceived tension between organismal biology and the

⁷ Ewens, 1993; De Winter, 1997; Crow, 2001, 2009; Sarkar, 2005; Borges, 2008.

then-nascent field of quantitative evolutionary biology.⁸ Based on a reading of previously unpublished correspondence, we show that the dispute was conducted within the context of a deep friendship between Mayr and Haldane that survived unscathed.

The remaining portion of the text is organised as follows. We begin by outlining the larger background within which the dispute was embedded; that requires giving a brief description of the history of population genetics and the Evolutionary Synthesis. Next we introduce the protagonists, explain the basis of their disagreement and contrast it with the level of friendship that they maintained in the face of fundamental scientific disagreements. This is evident from the letters they wrote; the exchanges ran from 1951 to 1964, when Haldane died. We cite diverse opinions on the dispute and point out that the rise of molecular biology contributed to organismal biologists' qualms about population genetics. The article concludes with a summing-up in which we comment on the different ways of assessing the role of theories and models in biology. The main text is interspersed with extracts from letters between Haldane and Mayr that chart their relationship during the period of the dispute, provide insights into their thinking about evolution and their feelings for each other. The correspondence is within specifically demarcated portions and can be read as a parallel narrative on its own.

Background

Mendelians and Biometricians

The rediscovery of Mendel's laws of heredity in 1900 was followed by a period of uneasy coexistence between what we would today consider two bedrocks of biology: the laws of Mendel and the Darwinian principle of evolution by natural selection. So much so, that many wondered whether Mendel's laws and natural selection had anything to do with each other at all. The upshot was that for a long time, students of evolution were divided into two rival camps.⁹ At the risk of some oversimplification, their views can be described as follows.

⁸ A sense of discomfort associated with mathematical reasoning and a concomitant reluctance to accept the validity of arguments based on it, is not entirely absent among whole-organism biologists today either. This is especially because of what are believed to be over-simplifications. For more on this see the "[Summing Up](#)" section.

⁹ Mayr, 1982; Provine, 1971 and 2001.

For the 'Biometricians' or 'Darwinists,' evolution occurred by natural selection along the lines explained by Darwin and Wallace. They believed that evolution took place quasi-continuously, in tiny steps. Each step was the result of selection acting on a set of pre-existing variations. The sequential accumulation of many steps over time led to differences in traits between ancestral and descendent populations; the differences were exaggerated versions of the traits that existed within a species. (A large increase in the average height over many generations could be an example of an evolutionary change that had been built on small differences in heights among the members of a species at any given time.) Over still more time, quantitative differences deepened to become qualitative differences. Accordingly, by studying variations within populations and correlations between relatives in respect of quantitative traits, Biometricians sought to infer the rules that would constrain the course of evolution. For them, the rate of evolution was determined by the rate of natural selection, not the rate at which variations (~mutations) arose. The qualitative or gross differences between individuals and varieties (that had occupied the attention of geneticists beginning with Mendel) appeared to be irrelevant for understanding how evolution worked. Framed thus, the Biometricians' point of view appeared to be in accordance with the Darwinian picture of evolution as a gradual process of change.

Against that, the Mendelians based their arguments on hereditary changes with gross effects that were easily observed. The changes were ascribed to abrupt alterations, mutations, in the particulate entities, genes, whose existence implicitly had been postulated by Mendel (though the words 'gene' and 'mutation' came much after him). Other than trivial modifications (like increased height), said the Mendelians, evolutionary change was a reflection of qualitative or discrete alterations in traits. The alterations were consequences of gene mutations: in essence, mutation *was* evolution. Therefore the rate of mutation, rather than the rate of natural selection, was the pacesetter of evolution. Mendelians asserted that the tiny changes that interested the Darwinians, and were required by the theory of natural selection, were irrelevant for what was important in evolution. Instead, the focus had to be on the major transitions that had occurred during evolution. According to them the transitions could have resulted from mutations of large effect. This implied, they said, that evolution in the large and evolution by natural selection were two different categories of phenomena.

Population Genetics

Starting from the early decades of the twentieth century, evolutionary biology began to acquire mathematical overtones. A set of models was developed in which the Darwinian picture of evolution was shown to be consistent with the laws of heredity discovered by Mendel. These models, associated primarily with the names of R. A. Fisher, J. B. S. Haldane, S. Wright, and S. S. Chetverikov, are a component of modern evolutionary theory and define a field of study known as population genetics.¹⁰ Some of the models were deterministic and made precise predictions whereas others included a consideration of stochastic effects, dealt in probabilities and led to statistical predictions. They showed that rather than being opposed to Darwinian evolution, the rules of Mendelian inheritance in fact provided just the underpinning that it required. J. T. Bonner puts it thus:

The tide turned with the rise of population genetics, in which R. A. Fisher, J. B. S. Haldane, and S. Wright used mathematics to show how selection and other factors which lead to change, could alter the frequency of individual genes in a population. This new approach was somewhat grandly called ‘the new synthesis,’ and T. Dobzhansky, A. H. Sturtevant, E. Mayr, and others did much to expand it to questions of how new species arise and to other global evolutionary problems.¹¹

Mayr gives a pithy description of what the models achieved: they showed that ‘there is no conflict between particulate (non-blending) inheritance, continuous variation, and natural selection.’¹² There were three principal reasons behind the success of these early models of population genetics. (a) They portrayed the process of evolutionary change in terms of a change in the genetic composition of a species. (b) They defined the genetic makeup of an individual in terms of the genes (strictly, alleles) at each locus in that genome, and the genetic composition of a population in terms of the relative frequencies of the different genes (again, alleles). (c) For practical reasons, mostly, they restricted themselves to treating situations in which different genetic compositions

¹⁰ The birth of population genetics preceded these models. A notable event was the recognition in 1908 by W. Weinberg and (some 6 months later) G. H. Hardy of an important implication of the conservation law alluded to earlier: in large, random-mating, Mendelian populations, genotype frequencies attain a stable equilibrium after one round of mating. See Provine (1971) for details.

¹¹ Bonner, 1996, p. 126.

¹² Mayr, 1982, p. 553.

at a single locus were assumed to be associated with different traits in the organism. This meant that the consequences for survival and reproduction of an individual's genetic makeup at one locus could be considered separately from the consequences stemming from its makeup at other loci.

Long after the Synthesis appeared complete, one of its leading contributors, Ernst Mayr, expressed doubts regarding the role played in it by population genetics (which by then had become an established field of research). His qualms had nothing to do with the Mendelian–Biometrician dispute. Instead, he worried that the models constructed by population geneticists had been too simple-minded, that they had ignored essential features of the link between genes and traits. Therefore, he asserted, the findings that resulted were of little value for understanding evolution. The gist of his criticism was that the models treated genes as independent carriers of hereditary traits, whereas in fact genes functioned as interacting complexes, not as independent entities. In a humorous analogy, Mayr drew an analogy between the population genetics approach to explaining evolution and counting genes as if they were differently coloured beans in a bag. J. B. S. Haldane, one of the founders of population genetics, contested Mayr's criticism forcefully in a famous publication.¹³ The exchanges between Mayr and Haldane, along with comments made at various times by other workers, constitute what has come to be called the beanbag genetics dispute (or controversy). The explicit part of the dispute pitted Haldane and Mayr on opposite sides of an important question: Just what non-obvious insights into evolution had come from the models of population genetics? There is an implicit part to the dispute, which touches on a more fundamental issue and remains unresolved. Namely, given the practical limitations of population genetics models, can they continue to help us in understanding the enormously complex evolutionary process while remaining compact and understandable?

The Protagonists

Ernst Mayr (1905–2005)

In the words of Walter Bock,

It is fortunate that Ernst Mayr has enjoyed such a long life, because he had to fit at least four major careers into it – that of an avian

¹³ Haldane, 1964.

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systematist, an evolutionist, a historian of science, and a philosopher of science. And he was successful in all of those careers, inside and outside ornithology.¹⁴

Mayr began his career as an ornithologist in Germany, migrated to the USA in 1931, achieved fame as an evolutionary biologist and, as mentioned, was one of the principal contributors to the Evolutionary Synthesis. He was instrumental in founding the journal “Evolution” which gave evolutionary studies a firm footing in biological research in the USA. Along with contributions from G. G. Simpson, Th. Dobzhansky, G. L. Stebbins and others, Mayr’s field studies and analyses made it appear that genetics and natural selection provided the most plausible explanation for a range of features of life on earth including biodiversity and the geographical distribution of plants and animals, and, in general, evolutionary change. Further information, including a full-length biography, can be found in the literature.¹⁵ Mayr wrote prolifically and continued to develop his view of evolution through a long life; “Animal Species and Evolution” is an acclaimed classic.¹⁶

J. B. S. Haldane (1892–1964)

Along with R. A. Fisher, Sewall Wright, and S. S. Chetverikov, J. B. S. Haldane was one of the founders of the mathematical theory of evolution, also known as population genetics. He is acknowledged as one of the most erudite and prescient biologists of the twentieth century. He was among the first to develop a mathematical theory of enzyme action and to make the link between biochemistry and genetics. Haldane was also a mathematician, Marxist, philosopher and superb populariser of science. Together with his wife Helen Spurway, a distinguished geneticist in her own right, Haldane migrated from Great Britain to India in July 1957. Anti-Imperial sentiments were part of the reason for leaving. In the beginning the two of them took up positions at the Indian Statistical Institute, Calcutta and worked there from July 1957 to May 1961. Thereafter Haldane established a research unit in Calcutta for just over a year and later moved to Bhubaneswar in Orissa where he died in 1964. Haldane revelled in controversy all his life. The Beanbag Genetics dispute, one of the best known, took place during his Indian period.

¹⁴ Bock, 2004.

¹⁵ Bock, 2004; Haffer, 2007; Mayr, 1980; Provine, 2004; Wilkins, 2002.

¹⁶ Mayr, 1963.

For more about Haldane, see the biographies by Clark¹⁷ and Dronamraju¹⁸ and shorter pieces by several writers.¹⁹ Haldane summarised his view of the evolutionary process in 1932 in a classic of his own²⁰ and continued to make major contributions to evolutionary biology over the rest of his life.

Haldane–Mayr Correspondence: (1) Before the Cold Spring Harbor Symposium

Ernst Mayr remained ignorant of Haldane's contributions for a surprisingly long time: "People have often asked me what impact Fisher, Haldane and Wright had on my thinking. My answer is quite embarrassing...I did not become aware of Haldane's work until about 1947."²¹ We do not know when Haldane came to know of Mayr. The two appear to have met for the first time in Princeton, New Jersey, in 1947 at an international conference held under the auspices of the US National Research Council at which Sewall Wright was also a participant²²; the "Princeton Conference" has become famous in the history of the Evolutionary Synthesis.²³ Their next meeting was in the summer of 1951. Being considered an enemy alien during the period of World War II, Mayr had been unable to travel outside the USA and had to wait until after he obtained US citizenship in December 1950.²⁴ But now he was going to be in Pavia, Italy, and wrote to Haldane on March 16, 1951:

Dear Haldane, I shall be in England in about the middle of May to the early part of June, and I hope I will have an opportunity to see you...I am planning to spend most of the spring and summer in Europe, and it will start with a visit to Pavia where I will lecture to Buzzati-Traverso's department.²⁵

¹⁷ Clark, 1968.

¹⁸ Dronamraju, 1985.

¹⁹ Maynard Smith, 1965; Wright, 1968; Crow, 1992; Nanjundiah, 1992; Bonner, 1998.

²⁰ Haldane, 1932 and 1990.

²¹ Mayr, 1980, p. 421.

²² *Ibid.*, p. 42.

²³ Mayr and Provine, 1980 and 1998.

²⁴ Haffer, 2007.

²⁵ Letter dated 16 March 1951 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 14.7, BOX 8, F 384; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

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Haldane was happy to learn that Mayr was to be in the neighbourhood and, in the summer of 1951 (surmised), extended a cordial invitation:

Dear Mayr, We shall of course be delighted if you can stay with us, as Prof. Norbert Wiener has recently done. But it is only fair to warn you that (1) Our flat is full of cats, and stinks vilely. (2) We are apt to work till midnight, so you would have to look after yourself to some extent... But bed and breakfast are yours for the asking, and we would like to have you very much if only for a few days. We have what may be a new idea about speciation, which I will discuss...My wife joins me in hoping you will spend at least a few nights with us (unless your FBI would object).²⁶

The allusion to the FBI must be read in the context of Haldane's well-known Marxist sympathies. After Mayr had enjoyed the company of the Haldanes in London, he wrote back on September 26, 1951: "I had a most profitable time not only in England but also in various other European countries, and I hope to derive benefit from the many stimulating conversations for years to come."²⁷ More letters passed back and forth. In one, dated November 15, 1951, Mayr tells Haldane what many others have felt before and since: "Yes, you are right that Darwin was perhaps the biologist who made the greatest contribution to geology. There is much in the *ORIGIN OF SPECIES* that is overlooked by everyone, even though it is as valid today as it was then."²⁸

There was a regular flow of letters between Haldane in the UK and Mayr in the USA until 1956. Haldane and his wife Helen Spurway moved to India in July 1957 and took up positions at the Indian Statistical Institute, Calcutta at the invitation of P. C. Mahalanobis, the Director. In spite of their distance, Haldane and Mayr were in regular touch, with Haldane discussing the research work in genetics being carried out in his unit at the Indian Statistical Institute (ISI) and each using the other to try out their ideas. In one of his early letters to Haldane after the move to India, Mayr vents his exasperation at all the travelling he is doing (presumably because it was the centenary of the

²⁶ Undated letter, inferred to be of 1951, from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 14.7, BOX 9, F 406; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

²⁷ Letter dated 26 September 1951 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 14.7, BOX 9, F 406; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

²⁸ Letter dated 15 November 1951 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 14.7, BOX 10, F 428; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

publication of “The Origin of Species”), mentions that he plans to visit him and, on April 13, 1959, highlights yet another instance he has come across of the importance of gene interactions – something that was to play an important role later in the beanbag genetics dispute:

...no one seems to give us poor evolutionists a chance to be lazy and inert in this year 1959. Travelling from one evolution conference to the next, I feel like the old-time Vaudeville performer...I shall celebrate the passing of this trying year by going to Australia and if all goes well, I hope to pass through India on my way home...I have long wanted to come to India where I have quite good friends and I hope this will finally be possible. Not the least reason will be to see you and Helen again...I recently...visited Maynard Smith and discussed with him his selection experiments. It is rather interesting to see how the interaction of genes becomes the central problem wherever one checks what they do in some genetic laboratory. I must say that University College didn't seem to be the same place without you and Helen.²⁹

The Dispute Anticipated

The issues that were to underlie the beanbag genetics dispute cropped up on at least two occasions before 1959. The geneticist and developmental biologist C. H. Waddington voiced his reservations about population genetics during a symposium organised in Oxford by the Society for Experimental Biology in 1952 and repeated them in his book “The Strategy of the Genes.” Waddington began by conceding that over the previous 30 years mathematical theorists and experimental naturalists had made use of the viewpoint of genetics to mount a successful attack on the problems posed by evolution and “may be taken to have reached their goal.” But, looking deeper, he found that the mathematical treatment “has not...led to any noteworthy quantitative statements about evolution;” equally, “Very few qualitatively new ideas have emerged from it.”³⁰ Haldane, who wrote the Foreword to the symposium volume, did not miss the chance to rebut Waddington. Picking up a theme that he was to return to later, he pointed out that some of the

²⁹ Letter dated 13 April 1959 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 6, F 731; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

³⁰ Waddington, 1953.

contributions of the mathematical theory had become so familiar that their origins had been forgotten. The most obvious case involved the disproof of a notion that had “a superficial appeal to common sense, for example that dominants must oust recessives.” He went on to list others: the conservation of variation (in the absence of mutation and selection) and its slow loss in small populations, the maintenance of deleterious genes in a state of balance in the face of adverse selection and the role of heterozygote advantage in preserving genetic polymorphism.³¹

A symposium on the theme *The Genetics of Population Structure* was organised by A. Buzzati-Traverso in Pavia in 1953 and was attended by a galaxy of evolutionists including Fisher. The comments of two among them illustrate our theme. Dobzhansky said that Mendel had been fortunate in finding genes that segregated independently (i.e. were not linked); otherwise, his results could have “confronted him with a problem which he would have been unable to solve” – the discovery would have been “premature.” Therefore, he concluded,

...it has been wise, I think, that most geneticists have occupied themselves for almost half a century with studies on clear-cut, discrete character differences produced by single or at most by few genes... ‘Bad’ mutants, which involved complex gene interactions or which did not manifest themselves in all individuals which carried them, were often observed but rarely studied since they were too difficult to work with. However, “studies on traits produced by interaction of numerous genes with individually small effects” were beginning, and it was becoming appreciated that “variable genes in the gene pool of a Mendelian population are often integrated in complexes.”³²

I. M. Lerner based his remarks on those of Dobzhansky. Addressing “The Current Status of Population Genetics”,³³ he asserted that

...we face a crisis in this field...Yet the basis of most formal analyses in population genetics today is still tied to what may be called the gene frequency approach...Our current understanding of genetics, however, leads some of us to consider, as noted by Dobzhansky, complexes rather than classical single genes as the significant units, temporary as they may be, in evolutionary processes.

³¹ Haldane, 1953.

³² Dobzhansky, 1954.

³³ Lerner, 1954.

Lerner said there were “three areas which must be explored to give us a clue as to where we are to go next.” The first was semantics, i.e., achieving a common understanding of the meanings of technical terms; the next was “quantification of the processes dealing with changes in the genetic compositions of populations;” and the third was a “synthesis between formal and developmental analyses.” It is noteworthy that the first item in Lerner’s list is at the heart of present-day arguments related to our understanding of the evolutionary basis of social behaviour. His third point of criticism, the absence of an explicit role for development in population genetics models, was to be stressed repeatedly in the future by Mayr and several others.

Mayr was a participant at the 1953 Pavia symposium but did not speak. Haldane was there too; his task was to give the closing address. He did so with gusto, evoking the greatness of Pavia and quoting liberally from Lucretius and Dante (both of them forerunners of genetics, he claimed) in the original. He regretted that “a piece of chicken bone ‘in questa gola’ [‘in this throat’] was removed with a skill” [that] “prevented my mortal remains from joining those of Spallanzani and Scarpa in your museum.” But in the course of entertaining his listeners Haldane omitted to comment on the scientific proceedings, admitting ruefully, “I fear that your great poets have led me astray, and that I have not said what was expected of me.”³⁴

The dispute was anticipated again during the 1955 Cold Spring Harbor Symposium, which was on the theme “Population Genetics: The Nature and Causes of Genetic Variability in Populations.” Dobzhansky gave an introductory survey in which he stated that the time had come for population genetics, which “was really launched in the thirties,” to expand its scope and develop a more realistic and more complex picture of the evolutionary process, albeit one that was “likely to displease those who like single-minded solutions.”³⁵ Mayr took up the thread in his concluding remarks and alluded to a new, inclusive population genetics that had not been fully developed yet.³⁶ Ironically (in view of what was to come later), Wright, who spoke in between, also emphasised what Dobzhansky and Mayr were getting at. Population geneticists knew they had to pay heed to it, he said: “Each gene replacement inevitably has extremely ramifying pleiotropic consequences.” Therefore “Evolution depends on the fitting together of

³⁴ Haldane, 1954.

³⁵ Dobzhansky, 1955.

³⁶ Mayr, 1955.

favorable complexes from genes that cannot be described as in themselves either favorable or unfavorable.”³⁷

Mayr Initiates the Dispute

The dispute proper began with Ernst Mayr's inaugural talk at the 1959 Cold Spring Harbor Symposium on Quantitative Biology, held in the Centenary year of the publication of "The Origin of Species." The theme was *Genetics and Twentieth Century Darwinism*; Mayr was also one of its organisers. Appropriately for the anniversary that was being celebrated, his presentation, entitled 'Where are we,' consisted of a survey of the status of Darwinism in 1959.³⁸ He mentioned early in the talk that there was a major omission in Darwin's theory, namely that it left open the question of how variations arose and how they were transmitted through heredity. It was well known that the first problem was sufficiently difficult to have made Darwin take recourse to ideas derived from Lamarck. As for inheritance, Mayr added, the work of Mendel and his successors filled the gap and led to the establishment of genetics as a science; the consequences for evolutionary biology were profound. He took advantage of the opportunity provided by the symposium to expand on the link between genetics and evolution and began by identifying three distinct phases during the development of the link.

The first phase, Mayr said, was inaugurated by Weismann's work. Weismann showed how implausible were the ideas of Lamarck, and went to establish "a new intellectual climate for genetic thinking." It was this climate, according to Mayr, that made it possible for the significance of Mendel's findings to be appreciated after they were rediscovered. Next he alluded to the confusion that had prevailed because of the difference in the way the Mendelians and Biometricians (Darwinists) saw evolution. The divergence was so vast that even T. H. Morgan had been misled into thinking that evolution occurred because of "occasional lucky mutations that happened to be helpful rather than harmful." In due course the two views were reconciled. Following the reconciliation, he pointed out, two more phases followed that marked the coming together of genetics and evolution. They were a phase of "classical population genetics" and one of the "newer population genetics." The classical period was also termed the beanbag period.

³⁷ Wright, 1955.

³⁸ Mayr, 1959.

It was a period of “gross oversimplification,” because “Evolutionary change was essentially presented as an input or output of genes, as the adding of certain genes to a beanbag and the withdrawing of others.” This was the first use of the term “beanbag.”³⁹

The problem with this approach was its ‘emphasis on the frequency of genes,’ with each gene being treated as if it was “an independent unit favoured or discriminated against by various causal factors.” In contrast, the third period of Newer Population Genetics “was characterized by an increasing emphasis on the interaction of genes,” to a mode of thinking that he had earlier described as the “genetic theory of relativity” (a phrase that did not take hold). Mayr conceded that the contribution of beanbag genetics was not to be totally disregarded. It was a “necessary step in the development of our thinking;” in fact “it restored the prestige of natural selection.” After paying this compliment, Mayr asked “But what, precisely, has been the contribution of this mathematical school to the evolutionary theory, if I may be permitted to ask such a provocative question?” He was alluding explicitly to the mathematical analysis and models of Fisher, Wright and Haldane. The absence of Chetverikov’s name – and more generally the work of the Soviet school – from much of the English literature pertaining to early population genetics is an example of how language and culture impinge on science. Elsewhere, for instance in his epic *The Growth of Biological Thought*, Mayr credited Chetverikov with being “way ahead of the western group in his much clearer recognition of the evolutionary importance of gene interaction.”⁴⁰

Haldane–Mayr Correspondence: (2) From Cold Spring Harbor Symposium to “Animal Species and Evolution”

The very first time Mayr used the term ‘beanbag’ appears to have been during the Cold Spring Harbor Symposium in June 1959. He had charged Haldane, Fisher and Wright with being “Beanbag Geneticists.” For more than one reason, Haldane may have not learnt of this; in any case he did not react at the time. Haldane could not respond to Mayr’s salvo at the 1959 Cold Spring Harbor Symposium on the spot because the US government had ensured his non-attendance by denying him a visa. He was excited in December 1959 at the imminent visit of Mayr to Calcutta and tried to tempt Mayr with the advantages of staying with

³⁹ *Ibid.*

⁴⁰ Mayr, 1982, p. 558.

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him by chalking out an attractive itinerary. The visit would take in the world-famous temples of Orissa with some bird watching thrown in; besides that (Haldane to Mayr, 30 December 1959), "...There are no strings on our invitation.... Of course if you like you can stay in Calcutta hotel. Part of one fell down recently. ...Our garden contains spiders which weave webs whose threads are arranged in rectangles. I bet they haven't got such a web in the Zoological Survey!"⁴¹

Mayr appears to have been the only visitor for whom Haldane thought of chalking out such an elaborate programme. As planned, he was the Haldanes's houseguest in Calcutta and appears to have enjoyed himself thoroughly in their company. Haldane's regard for his visitor is evident from a letter he wrote on 15 March 1960 to the Mayor of Calcutta. While passing on Mayr's letter of appreciation regarding the Calcutta Zoological Gardens, he acquaints the Mayor with the eminent status of his visitor: "I may remark that Prof. Mayr is generally regarded as one of the three or four leading students of birds and ranks very high as a systematic zoologist. He occupies the most famous chair in the United States..."⁴²

All the signs are that the visit went off with Haldane remaining in the dark about Mayr's talk at that year's Cold Spring Harbor Symposium; as the 1953 Society for Experimental Biology volume shows, negative comments on his work provoked a quick response. It is hard to imagine him being so warm and hospitable towards a person who had just termed him a "Beanbag Geneticist," which strengthens the case for believing that Mayr's comments were yet to reach him.

In December 1960 Mayr came across an idea of Haldane's that was to loom large in the dispute. In a celebrated paper, among the earliest by him to be published with an Indian address, Haldane had advanced the notion that there would be a 'cost' of natural selection, also referred to as a "genetic load"⁴³ (H. J. Muller developed the concept independently). He was trying to draw an evolutionary lesson from a common experience of breeders: selection for many desirable traits at the same time was next to impossible (because it would be next to impossible to maintain a sufficiently large breeding population generation after generation). The lesson was this: if evolution acted via substitutions, acting

⁴¹ Letter dated 30 December 1959 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 6, F 731; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁴² Letter dated 15 March 1960 from J. B. S. Haldane to Mayor of Calcutta, India (No. NLS, MS-20538, F 192-206; National Library of Scotland, Edinburgh, UK).

⁴³ Haldane, 1957.

independently, of deleterious alleles by beneficial ones at a large number of loci – that is, natural selection weeded out the deleterious alleles – and if the population was not to crash, a cost would be demanded of the fittest individuals by way of extraordinarily high fecundities.

Apart from testing out ideas on each other, the two of them regularly exchanged published articles. On one such occasion, in the course of writing on 2 January 1961 to thank Haldane for some reprints, Mayr asked a question about the ‘cost.’ Would it not be significantly lowered if there were strong interactions between the fitness effects of genes at different loci? This was precisely the issue that others would raise later:

Your shipment of reprints reached me on Christmas eve and was my Christmas present that I enjoyed the most...I am particularly glad to have your paper on the cost of natural selection which I had of course read soon after it had come out. I think it will form the basis of a lot of future investigations...A second point that puzzles me is the effect of synergistic versus antagonistic interactions of genes. In view of the fact that no gene has an absolute selective factor, the contribution of a gene to mortality may be greater when it is combined with one or more other ‘bad’ genes than when it is combined with fitness-increasing genes. As a result a single case of genetic death may simultaneously eliminate several deleterious genes from the population. Wouldn’t that change your calculations?⁴⁴

Haldane’s reply of 11/12 January 1961 started by conceding that he was in the process of coming to grips with the various ways in which natural selection can exact a cost – some that need to be thought through to this day, as it happens – and ended with a swipe at US visa policy:

I am still thinking about the ‘cost of natural selection’ or the ‘substitutional load’...I have just, as you know, been awarded the [US] National Academy’s Kimber Medal. I should like to come in April and collect it. But when I last applied for a visa to your country I was told to list all organisations of which I had been a member since the age of 16, with dates of entering and leaving them. I regret that I do not know in what year I joined the National Mouse and Rat Club, to mention only one. And I think a scientist should go thru the motions of telling the truth. So unless your new

⁴⁴ Letter dated 2 January 1961 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

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State Department takes action, I fear I can't come. But if everybody had scruples of this kind, civilised life would be impossible.⁴⁵

Mayr continued to plug away at conceptual issues associated with the concept of 'cost.' He was going to raise them in a forthcoming book, he wrote on February 21, 1961, evidently referring to "Animal Species and Evolution":

I have prepared a first draft of a discussion on genetic load for my forthcoming book and am enclosing it for criticism. Perhaps this will make some of the questions in my last letter little clearer. The relativity of fitness and the possible synergistical action of favorable as well as deleterious genes is not sufficiently coped with in published calculations. Our interest in questions of this sort is so recent that we still lack the pertinent facts.⁴⁶

Haldane's response was that one had to be cautious about drawing inferences from calculated 'loads;' he had made an estimate in the case of *Drosophila melanogaster* and he and his colleagues in Calcutta were trying to carry out a calculation involving humans (Haldane to Mayr, 3 March 1961):

If I were you I would perhaps make the point that a 'load' even of 50% may be slight if it occurs early enough in life. You nearly make it on p.3. but not quite...If, say, lethals killed the same number during pupation, this would be much 'heavier.' The inviable eggs may even be eaten by their brothers and sisters, and inviable babies by their mothers... Dronamraju... [and]...Meera Khan...now have much better figures based on hospital patients who may be expected to be rather inbred, and school children, who may be expected to be rather outbred, 7.3% of all marriages are with nieces, 16.8% with first cousins. I think, if we can get support for this work, we may be able to estimate some loads. But it is less trouble to do a job of work than to cadge for the cash. I haven't thought much about loads lately, as some broken bones have been troubling me.⁴⁷

⁴⁵ Letter dated 11/12 January 1961 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁴⁶ Letter dated 21 February 1961 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁴⁷ Letter dated 3 March 1961 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

Mayr's answer of 16 March 1961 showed that he would not let go of a problem that – he thought – could undermine the idea itself:

Yes, the difference between early and late mortality is precisely the one I was trying to make in my own comments, and this is why I think that 'cost of evolution' is less severe than you suggest. If you make the further assumption, which I think is not altogether unreasonable, that various fitness-reducing factors are synergistic, you may have quite an elimination of genes and genotypes without any real threat to the survival of the population...

My main point really is that one must eventually go beyond the preliminary stage of assuming that genes have constant and absolute selective values, an assumption we all know not to be realistic but into which we are being forced by the simplifying value of the assumption. My feeling is that by operating with 'average selective values' of genes, we introduce quite unrealistic models into our calculations.⁴⁸

For the moment this discussion petered out. Haldane, who had become an Indian citizen in the meanwhile, offered advance regrets in a letter of 19 April 1961 that he would be unable to collect the Kimber Medal in person (Haldane to Mayr): "I am very sorry I shan't be able to get to Washington on April 24th...between the Indian and American bureaucracies, I doubt if I could have got a visa. The Indian one has taken nearly a year getting me Indian nationality."⁴⁹

The 'cost of natural selection' hypothesis was to have a curious consequence. Quantitatively-minded evolutionists showed later just what Mayr had tried to do in the letters cited above (see notes 44–48). Haldane's calculation, though mathematically correct, had hinged on the crucial assumption that selection acted independently at different loci. It turned out that Haldane had been wrong in believing that the result was general. With more plausible models, for example interactive fitness effects or 'truncation selection,' the cost could be negligible or non-existent.⁵⁰ However, by taking Haldane's result at face value, Kimura drew an unexpected inference.⁵¹ Namely, it was unlikely that

⁴⁸ Letter dated 16 March 1961 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁴⁹ Letter dated 19 April 1961 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 7, F 761; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁵⁰ Maynard Smith, 1968; Ewens, 1993.

⁵¹ Kimura, 1968a.

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populations could carry alleles that lowered fitness at very many loci – precisely because the cost of doing so would be impossibly high. Therefore, he concluded, most mutations must be neutral. Thus the neutral theory of molecular evolution, arguably the single most significant contribution of population genetics theory to our understanding of the evolutionary process to come from the post-Synthesis period, was based on a less than firm ‘beanbag genetics’ foundation.

Unhappy with the way the Indian Statistical Institute was being run, Haldane and Helen Spurway resigned from it in the year 1961 and established a “Genetics and Biometry Unit” under the auspices of the Council for Scientific and Industrial Research (CSIR), initially at their residence itself. Mayr was happy to learn about the move and, when he wrote to Haldane at his new work place on 1 March 1962, made the first mention of his book “Animal Species and Evolution”:

I am delighted to see that you are well established at your new little empire (or shouldn't I use such a dirty word)... I am glad that news from Helen and you is so cheerful. There is such a pleasure in doing straight forward research...I am most anxious to get back into it after working for so many years on a book manuscript. The book is now just about finished and has to be delivered to Harvard University Press on April 15th. You won't find much in it that is new to you, but I have made a real effort to sort and present systematically a vast amount of scattered information and theory about species and about evolutionary phenomenon on the species level. I hope, it will be considered for what it is, a progress report, and that it will stimulate people to continue where I leave off. I am always afraid that people might consider as final, what is one's provisional temporary conclusion.⁵²

Things did not work out with CSIR either. The Haldanes made yet another move by July 1962 and set up the ‘Genetics and Biometry Unit’ once again. This time it was at Bhubaneswar, with the help of the then chief minister of Orissa, Biju Patnaik. Mayr wrote on 19 November 1962 when he learnt about the move and gave a hint of what was to come:

I had not heard about your moving to Bhubaneswar until I received your reprints...I still remember with great pleasure my visit to Bhubaneswar under your guidance...I do hope you find

⁵² Letter dated 1 March 1962 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 8, F 790; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

happiness in these auspicious surroundings. I have just completed reading the galley proof of my Animal Species and Evolution and I hope that it will be available by about April next spring. I am sure you will find some things in it that will interest you and others with which you will disagree...I wanted to get away from the atomistic treatment of populations as samples of gene frequencies (independent of each other so to speak), and I had to be careful not to say anything that would suggest that I was in sympathy with holistic or finalistic ideas which, of course, I am not. Well, you will see in due time.⁵³

Considering the adverse remarks that the book contained, it is revealing that Mayr kept discussing it. In a letter of 25 February 1963 he announced his intention to send a proof copy for review. Evidently he was confident that Haldane would take scientific criticism in his stride:

I have managed to induce Harvard University Press to send you a set of page proof of my Animal Species and Evolution. They promised to send it by airmail and thus you will have a review copy long before anyone in England or continental Europe. I have also asked them to add proof of the bibliography, which should be rather useful to your students. As you will notice, I have tried to counteract the modern trend to forget all about the pioneers. In a number of areas I have made a real effort to trace back ward, the development of a concept to its earliest beginnings. I hope you and Helen will enjoy reading the volume and will not find too many things in it that you will have to disagree with.⁵⁴

Mayr's Comments in *Animal Species and Evolution*

The problem with the Mendelian viewpoint, Mayr reiterated in the book,⁵⁵ was that it restricted itself to a consideration of individual genes and their relative numbers:

⁵³ Letter dated 19 November 1962 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 9, F 805; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁵⁴ Letter dated 25 February 1963 from Ernst Mayr to J. B. S. Haldane (No. HUGFP, 74.7, BOX 9, F 820; Pusey Library, Harvard University Archives, Cambridge, MA, USA)

⁵⁵ Mayr, 1963.

When dealing with several genes, the geneticist was inclined to think in terms of their relative frequencies in the population. The Mendelian was apt to compare the genetic contents of a population to a bagful of colored beans. Mutation was the exchange of one kind of bean for another. This conceptualization has been referred to as ‘beanbag genetics’... Work in population and developmental genetics has shown, however, that the thinking of beanbag genetics is in many ways quite misleading. To consider genes as independent units is meaningless from the physiological as well as the evolutionary viewpoint. Genes not only *act* (with respect to certain aspects of the phenotype) but also *interact*. (p. 263)

The essence of speciation, as we now realize, is the production of two well-integrated gene complexes from a single parental one. All early attempts to explain the genetics of speciation missed this essential point, being concerned entirely with the problem of the origin of difference...It is now evident that there is only one situation in which a gene pool can be completely reconstituted genetically (with reference to a parental population) while all of its elements remain well integrated and co-adapted: spatial isolation...Why isolation was needed remained a puzzle until the genetics of integrated gene complexes had replaced the old ‘beanbag’ genetics. (p. 518)

And on p. 535:

The genetic revolution in peripherally isolated populations has been interpreted, so far, in terms of ‘beanbag genetics,’ in terms of shifts in gene frequencies. Such an interpretation is in distinct contrast to the belief of many early cytogeneticists that speciation is the result of a structural repatterning of chromosomes.

Mayr had enlarged the scope of his original complaint: besides its other failings, beanbag genetics could not explain the appearance of a new species, whether fuelled by spatial isolation (a means favoured by Mayr) or by sudden chromosomal changes. He seems not to have known that Haldane had said as much 30 years before⁵⁶: “[speciation] may take place as the result of the isolation of a small unrepresentative group of the population...” (p. 102); and “...a successful evolutionary step rendered a new type of organism possible, and the pressure of natural selection was temporarily slackened ...Another possible mode

⁵⁶ Haldane, 1932 and 1990.

of making rapid evolutionary jumps is by hybridisation...this may lead to the immediate formation of a new species by allopolyploidy” (pp. 104–105). Mayr’s criticisms were repeated in print many years later, with more detail, in the re-written version of the book *Populations, Species and Evolution*,⁵⁷ that was published after Haldane’s death.

Basically, Mayr was repeating a number of things that he and others had been saying over the years. The phenotype, and so fitness, depended on the genotype and its interactions with the environment. Therefore models needed explicitly to incorporate the causal processes by which phenotypes arose, in other words development. It was an oversimplification to reduce the system to one of single gene effects. Not only was the effect of a gene dependent on the action of other genes, the fitness associated with the phenotype depended on other phenotypes. On top of everything, the tools of population genetics were simply unable to tackle the most important evolutionary problem of all, speciation – not to mention the appearance of the higher orders. The views of Dobzhansky and Lerner, quoted already, strongly influenced Mayr’s thinking. So did the experimental demonstration by Mather of the complexities that showed up in selection for (apparently) a single trait. He was especially struck by a famous study⁵⁸ on selection for changing the number of bristles on the abdominal segments of *Drosophila melanogaster*. The findings were striking. Many genes were involved in bristle development; the “wild type” contained sufficient genetic variability to make it possible to select for significant changes in both directions; and selection led to completely unexpected consequences, among them being effects on fertility, fecundity and survival. The implication was that even straightforward directional selection for a simple trait involved a multitude of genes and interactions with many other traits.⁵⁹

Haldane–Mayr Correspondence: After “Animal Species and Evolution”

A short break followed in the correspondence between Haldane and Mayr. As seen, Mayr had reiterated his qualms about population genetics theory in “Animal Species and Evolution.” It was when Haldane was going through the page proofs of this book that he was forced

⁵⁷ Mayr, 1970, pp. 156, 162, 183, 297, 367.

⁵⁸ Mather and Harrison, 1949.

⁵⁹ Mayr, 1963, pp. 285–287.

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to confront the full force of Mayr's pejorative terming of Fisher, Wright and himself as 'Beanbag Geneticists.' In addition to the proofs, Haldane may have read Mayr's Cold Spring Harbor Symposium talk by then and, belatedly, felt the sting. This woke him up:

Thank you for the proofs, which I am reading. Whether people agree with your conclusions or not, your book will be an invaluable guide to the literature. As a "bean-bag geneticist," I think your view of a species may be a little too physiological and not historical enough. No doubt the various genes (as regards frequency and location as well as molecular pattern) have to fit together to form, if not an adaptive peak in Wright's sense, a range of such peaks, separated at most times from other such ranges by deep "valleys". But on reading you, I sometimes get the feeling that you think we could calculate the species if we knew enough about the genes. My guess is that existing species are only a small fraction of those which might have been made up with the genes available in a genus or family, and that the reasons why we have just these species are largely historical.

Haldane continues,

As will be seen from p. 400 of the enclosed, I think your definition of a species, though not your description of it, is a little too futuristic for my taste. I tried to develop the philosophical side of my view of species, in an article called 'Differences' (Mind, LVII N. S. July, 1948, pp. 294–301), but I have no offprints left.⁶⁰

As he had done before in his book,⁶¹ Haldane is saying here that besides isolation and adaptation, the formation of a new species might involve contingent ("historical") factors; his view of evolution was not restricted to natural selection.⁶² Now Haldane the scientist made way for Haldane the friend: "We are within about 1 km of the area where you saw larks and other birds when you were here. Perhaps you will come again. But you might find us unhospitable during day light." The next letter, on 8 May 1963, elaborated on the theme:

⁶⁰ Letter dated 6 April 1963 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 9, F 820; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁶¹ Haldane, 1932 and 1990, pp. 104–105.

⁶² For example: "...where natural selection slackens, new forms may arise which would not survive under more rigid competition, [leading to the appearance of] many ultimately hardy combinations;" and "Another possible mode of making rapid evolutionary jumps is by hybridisation" (Haldane, 1932).

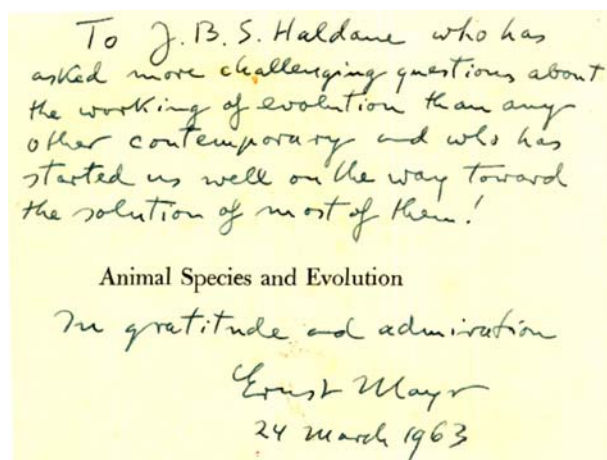
I am an unrepentant ‘beanbag geneticist’. Non-mathematicians often fail to realise the complexity of behaviour and sometimes the self-regulatory capacity of material systems composed of simple components...Newton thought the creator had put the beans (Sun, planets, and satellites) in the bag and given it a shake. But he thought the system would lose its regularity, and after a few thousand years the creator would have to give it another push. Laplace showed that it would continue for at least 100,000 years, (a very long time in those days) and therefore informed Napoleon that he had no need of the hypothesis of super-natural interference. We still don’t if it is stable for periods over 10 years, probably because we aren’t sure enough about relativistic corrections. I have got back to beanbag genetics in a big way, largely because I have got a colleague, Jayakar, who can correct my algebra. We find that there are a whole lot of conditions other than superiority of heterozygotes which will conserve polymorphism on a reasonable scale. 30 years ago, I showed that mutation would not, unless selective differentials were as small as mutation rates, but that migration might do so. We can now give the conditions as to migration rather more concretely.

The theory, which we are working out, of just what happens when an initially ‘unfavoured’ genotype gradually increases its selective value, is very tricky. It seems that the population may change rather suddenly, even if the relative fitness is only increasing slowly, and the selection of ‘modifiers’ may make this change still more sudden. (At this place a marginal note by Mayr reads ‘no longer bean-bag!’). Unfortunately even when selection is weak we need Bessel functions, which occur in the theory of vibration of drums. But we are beginning to see what may happen when climatic conditions change slowly. We have just worked out a fairly comprehensive theory of what happens under selection of constant intensity when this is fairly strong (as it doubtless is when a new niche is occupied and there is no immigration from the old one). For this we need automorphic functions of a kind which were fashionable in France about 1920. I may of course be hopelessly out-of date in my approach. I am sure bright boys like Jim Crow think so. But it seems to me that mathematical genetics are still about the stage of $s = \frac{1}{2} ft^2$...and that the mathematicians who come in from time to time are interested in inessentials, or shall we say, topics whose biological importance is not obvious. If I could

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have devoted my life to the mathematical theory of evolution, I might by now be able to tell you a little more about populations. But I have so much else to do, even as a mathematician.⁶³

Haldane's advance copy of "Animal Species and Evolution" arrived with a fulsome handwritten dedication from Mayr:



To J. B. S. Haldane who has asked more challenging questions about the working of evolution than any other contemporary and who has started us well on the way toward the solution of most of them!

Animal Species and Evolution

In gratitude and admiration

Ernst Mayr
24 March 1963

At the time that he received the book in Bhubaneswar, he may have been suffering from the colorectal cancer of which he was to die next year. There was a regular exchange of friendly letters between the two of them during this period, but Haldane was simultaneously preparing to attack Mayr. He thought he was writing on behalf of the triumvirate (not knowing, perhaps, that Wright had answered Mayr in 1960; Fisher had died in 1960). This time, on 3 June 1963, his stand reflects an 'attack is the best form of defense' attitude:

I have also completed a much more serious attack on you, entitled 'A defense of beanbag genetics'. This is intended for 'Perspectives in biology and medicine'. I may say that from defense I pass to counter-attack". In even-tempered language he continues "However I am going to get it typed, and then look at it again after three months or so, to see if I find any sections of it unclear or unfair or whether perhaps some new arguments have occurred to me. Here is an example of a counter-attack. On p. 191 of 'Animal Species and Evolution' you suggest that I did not believe in strong selection till 1957. In 1924 (Trans. Camb. Phil. Soc, recently reprinted by

⁶³ Letter dated 8 May 1963 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 9, F 820; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

Comstock and Robinson of N. Carolina) I calculated that the mutant Carbonaria of *Biston betularia* [sic] conferred an advantage of about 50%. This was beanbag genetics, and nobody took it seriously for 30 years.”

Haldane goes on,

I may conceivably be in U.S.A. in October. Some of the N.A.S.A. boys have asked me, but I doubt if I shall get a visa. If I am there, I might be able to see you. But it is easier for you to get here. My house is about 1 km from the place where you saw the larks in the early morning.⁶⁴

Scientific disagreement did not come in the way of their friendship. Mayr valued this equally, and in the course of commenting on Haldane’s ‘Origin of Lactation’ paper, goes onto tell Haldane on 18 June 1963 that he is prepared to receive his response on the beanbag genetics issue:

I shall receive your ‘attack’ on me philosophically. In a big volume like the one I have written, it is quite impossible to avoid short-cuts and generalizations. For instance, I had your 1924 paper in an earlier draft, but took it out since you refer to it in your later papers, and I had to streamline my over-long bibliography. I wonder whether other readers would also come to the conclusion that ‘I suggest that you did not believe in strong selection until 1957’ The whole point I tried to make was that around 1930, the emphasis was on effect of slight differences in selection pressure and that this led many non-geneticists into making unrealistic assumptions.⁶⁵

Haldane’s “Defense”

Haldane gave a spirited reply to Mayr’s provocations in a publication entitled *A Defense of Beanbag Genetics*.⁶⁶ As far as the two of them were concerned, the public controversy ended there. An obvious question is why it came so late. As we have suggested, the answer may be that

⁶⁴ Letter dated 3 June 1963 from J. B. S. Haldane to Ernst Mayr (No. HUGFP, 74.7, BOX 10, F 836; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁶⁵ Letter dated 18 June 1963 from Ernst Mayr to J. B. S. Haldane (No HUGFP, 74.7, BOX 10, F 836; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁶⁶ Haldane, 1964.

Haldane had not read the Cold Spring Harbor Symposium volume when it came out and was simply not aware of Mayr's comments of 1959. Because of a lack of up-to-date library facilities at the Indian Statistical Institute, Haldane seems to have been ignorant of Wright's 1960 response in the *American Journal of Human Genetics* too (see next section). Oddly, none of his friends would appear to have passed on Mayr's negative assessment of population genetics to him, either in correspondence or in person. Based on the evidence available, the impression is that he first got to know of Mayr's attack in 1963, when Mayr himself sent a page proof copy of *Animal Species and Evolution* with a view to getting it reviewed.

Haldane begins with an introduction to the 'beanbag approach'; even though he uses the word Defense in the title, his style is anything but defensive. He starts out disarmingly, by appearing to agree with Mayr, and goes to the extent of denying that 'the mathematical theory of population genetics is anything at all impressive, at least to a mathematician.' As an example, he cites the large number of simplifying assumptions used in very early work and points out that even with those assumptions, the mathematical difficulties were huge. Solutions could be found in certain limiting cases only: 'If we had solved such problems, our work would be impressive.' He adds that professional mathematicians who have 'interested themselves in such matters...have been singularly unhelpful (because they have been concerned more with formal issues, such as proving that a solution exists).' Haldane's message is that while formulating scientific problems in mathematical language, one should be careful not to get diverted by the mathematics. The important thing is to work out *useful* solutions and avoid getting entangled by purely mathematical issues. Others have pointed out⁶⁷ that Haldane's attitude to the use of mathematics in biology was essentially utilitarian, which is not to say that he did not enjoy doing mathematics for its own sake. This part of the article ends by invoking classical precedents for the formulation of the beanbag genetics concept – just as he had done a decade earlier in the Pavia meeting.⁶⁸ He begins with descriptions of a possible material basis of heredity:

Now let me try to show that what little we have done is of some use, even if we have done a good deal less serious mathematics than Mayr believes. It may be well to cite the first formulation

⁶⁷ Crow, 1992; Maynard Smith, 1992.

⁶⁸ Haldane, 1954.

of beanbag genetics. This was by the great Roman poet Titus Lucretius Carus, just over 2000 years ago... A free rendering is: 'since parents often hide in their bodies many genes mixed in many ways, which fathers hand down to fathers from their ancestry; from them Venus produces patterns by varying chance, and brings back the faces, voices, and hair of ancestors'. Very probably, the great materialistic (but not atheistic) philosopher Epicurus had expressed the theory more exactly, if less poetically, in one of his last books...What is important is that whether he called them primordia or even seeds, he always thought of them as a set of separable material bodies.

Next, Haldane points out that Mendel and his successors discovered quantitative regularities in the way the material entities behaved, which made it possible to develop a science of heredity: "When Mendel discovered most of the laws according to which Venus picks out the hidden genes from the mixture, and Bateson and Punnett further discovered linkage, we could get going; and it was Punnett (5) who first calculated the long-term effect of a very simple program of selection."

The second part starts with "Now let me begin boasting" and carries onto say "So competent a biologist as Professor L. T. Hogben (6) has recently written, 'The mutation of chromosomes or of single genes is admittedly the pace-maker of evolution.' A strong verbal argument could be made out for this statement." Haldane continues his reply thus: "The estimation of human mutation rates, which is a by-product of my mathematical work, has since assumed some political importance. Had I devoted my life to research and propaganda in this field, rather than to expanding the bounds of human knowledge, I should doubtless be a world-famous 'expert.'"

He goes onto enumerate some of the successes of classical population genetics that were achieved thanks to the "beanbag" approach. The list includes the following. (i) What determines the rate of evolution? A naïve analysis might tell us that it could be the rate of mutation, precisely because it is so much smaller than any other rate that one can imagine as being relevant (e.g. genetic exchange or reproduction). Thus mutation would seem to act as the "pacemaker" of evolutionary change. Mathematical analysis confounds this expectation: it shows that the rate of evolution depends strongly on the population size and the strength of natural selection. In fact, for sufficiently large populations, the rate at which a favourable gene spreads is determined essentially by the strength of selection. By applying his theory to the celebrated case of industrial melanism, Haldane showed that when the pressure of

selection was intense, evolution could occur far more rapidly than most would have thought possible.

There was to be a posthumous final shot at Mayr. Haldane and S. D. Jayakar (writing independently, and, interestingly, in Haldanian style) reviewed “Animal Species and Evolution” in *Journal of Genetics*,⁶⁹ as did Helen Spurway, for the *Journal of Bombay Natural History Society*.⁷⁰ Haldane started off by calling it “the best book of its kind...indispensable to any animal biologist...for the extremely stimulating ideas to be found in every chapter,” though “Mayr’s arguments have not convinced me that sympatric speciation has never occurred, though I think he has demonstrated its rarity.” When it came to population genetics, the language was forthright: “Mayr seems to me greatly to overestimate the simplicity of this subject...I have attempted elsewhere (Haldane, 1964) to defend beanbag genetics. I think Mayr has failed to grasp the extreme complexity of the results which are possible if one starts from simple probabilistic axioms.”

Wright’s Response to Mayr

Contrary to Haldane’s belief, Sewall Wright had in fact responded to Mayr. Wright was one of the participants in the 1959 Cold Spring Harbor Symposium and even chaired a session. Strangely, he did not make a presentation. But he seized the opportunity to present his side the very next year in a long review of the Symposium volume in the *American Journal of Human Genetics*.⁷¹ Not surprisingly, he had a lot to say about the *Where Are We* article, and its gist was that Mayr had got it all wrong. First, in discussing lines of research in population genetics since 1900, he “had seriously misrepresented the roles of these various lines as well as the contributions of the one with which I am most familiar;” his own “recollections of the attitudes of naturalists and geneticists [during the Mendelian period] towards natural selection...differ considerably from Mayr’s statement.” Referring to “beanbag genetics,” Wright continued: “To demonstrate that progress by selection is restricted to the net effects of genes in the combinations in which they enter is not to ignore interaction as Mayr seems to suppose;” if anything, “the treatment of interaction systems was the central theme of most of the ‘classical’ population genetics.” In effect, Mayr and

⁶⁹ Haldane, 1965 and Jayakar, 1965.

⁷⁰ Spurway, 1965.

⁷¹ Wright, 1960.

Wright agreed that gene interactions existed and could not be neglected. But whereas Mayr drew the further inference that the interactions were so strong that they made any discussion of single-gene effects inconsequential, Wright pointed out that treating genes singly was not the same as ignoring the effects of other genes. An extreme version of the single gene view is associated with Fisher rather than Wright or Haldane. It holds that the evolutionary history of most sexually reproducing organisms has been so long that there has been sufficient time for recombination to throw up an enormous number of genotypes. Every gene has been put to the test in essentially every possible genetic background. Therefore, it is meaningful to consider the (averaged) effects of single genes and build on them.⁷²

Wright hammered home his rebuttal of Mayr in a survey of the foundations of population genetics⁷³ and continued to do so over the next two decades.⁷⁴ Later, Mayr acknowledged that he had been less than fair to Wright. He confessed to Provine⁷⁵ that he had not made a careful study of the articles or books by Haldane, Fisher or Wright when he first attacked their work: “He was being controversial, to promote ‘better science.’” In the same interview to Provine, given in 1986, Mayr revealed that he too had been a “beanbagger” in 1942, and regretted having classified Wright as one. Wright had a background in experimental genetics, was familiar with correlations between gene effects and polygenic inheritance, and had enjoyed a long and fruitful collaboration with Dobzhansky on modelling the evolutionary consequences of genetic variation in natural populations. Considering all that, the lack of a proper appreciation of Wright’s way of looking at evolution remains a puzzling omission on Mayr’s part.⁷⁶

Haldane–Mayr Correspondence: Final Letters

The subsequent correspondence mainly involved ongoing research until Mayr learnt of Haldane’s colon cancer. Haldane had dashed off a

⁷² Fisher, 1930 and 1958.

⁷³ Wright, 1967.

⁷⁴ Provine, 1986.

⁷⁵ Provine, 2004.

⁷⁶ On the other hand a reviewer of this paper pointed out that given the less than smooth course of Mayr’s previous interactions with Wright, the omission is not all that puzzling.

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humorous poem about it (“Cancer’s a Funny Thing;” see <http://www.oatridge.co.uk/Haldane.htm>). Mayr’s reaction was sent on 20 April 1964:

I got hold of your ‘ode on cancer,’ which amused me with its Shavian sense of humour. I do hope that you are not too uncomfortable...I hope to pass through London this coming July, and will be very much looking forward to seeing you then, if you should still be in England.⁷⁷

Haldane was feeling homesick and wanted to get back to India after his surgery. In his reply dated 2 May 1964 he showed that he had retained both his sense of humour and his spirit: “I am pretty well alright, except that my colostomy has not learned to cope with the diet here in a regular manner. This means that I can’t yet travel around much, a very great advantage if one wants to work, as I do.” He continued with details of the work being done by Helen Spurway and Jayakar on birds. But ‘beanbag’ was not forgotten:

Of course, we do plenty besides bird watching. I do beanbag genetics...I learn from the local press that I have been elected to the [US] National Academy...The election can be explained on several grounds, e.g. 1) They thought I was dying of cancer, and wished to solace my last moments 2) ...After your remarks, the beanbaggers felt something must be done. And so, one might go on... But I now think it would be better to recognise younger men than myself.⁷⁸

By now ‘A Defense of Beanbag Genetics’ had been accepted for publication by ‘Perspectives in Biology and Medicine’ and may even have appeared in print; the issue is dated ‘Spring 1964.’ The editor enquired if Mayr would like to respond; he was disinclined to do so. Instead, he offered Haldane an olive branch when he wrote on 3 June 1964:

The editor of Perspectives in Biology and Medicine has asked me to respond to your statement on beanbag genetics, but I am not sure that I will do so. Obviously, most of what you say will be fully

⁷⁷ Letter dated 20 April 1964 from Ernst Mayr to J. B. S. Haldane (No. HUGFP 74.7, BOX 11, F 852; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁷⁸ Letter dated 2 May 1964 from J. B. S. Haldane to Ernst Mayr. (No. HUGFP 74.7, BOX 11, F 852; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

endorsed by me also. It is all a matter of emphasis. A certain amount of beanbag genetics is the necessary basis for all else, but on the whole, beanbag genetics is singularly unsuitable to explain any but the most elementary evolutionary phenomena. Penetrance, as you rightly remark in your letter, is a case in point. The recent models developed by Jacob and Monod, and others, about regulating genes are further substantiating arguments. The enormous increase in the amount of DNA among eucaryotes, most of it apparently not used for structural but for regulating genes, is still further evidence. It is no use to argue about trivia, but I still believe that beanbag genetics in many cases had a detrimental rather than beneficial influence on evolutionary thinking. You, yourself, without using such terminology, have called attention to this in many of your papers.

Mayr went on to heap praises in what seems to have been his last letter to Haldane:

I realize that your election to the National Academy is not an honor to you but a removal of a disgrace from us...I do not know whether this will please you or not, but I can assure you that you have been for years the leading candidate of the biologists. It has been a great source of satisfaction for all of us that your election was finally ratified. Hence even if the election should not mean a thing to you, I can assure you that it means a lot to us.⁷⁹

When he wrote next Haldane requested Mayr not to write directly to him anymore, as he was getting rather weak, and pointed out some features of Spurway and Jayakar's field work. In Mayr's response of 21 October 1964, which was addressed to Helen Spurway, he referred to Haldane as a polymath:

I still remember the Pavia meeting, not because Haldane almost choked with a chicken bone in his throat or because of his incredible virtuosity with verses from Dante's *Commedia Divina*, but because Haldane was the only one of the older geneticists present, who fully appreciated what the younger ones were talking about. R. A. Fisher disappointed me at the time by simply resisting the new ideas. Haldane accepted them at once (so far as they were sound) and asked meaningful questions as to where to go from here. This flexibility of his mind, no doubt is the reason for his

⁷⁹ Letter dated 3 June 1964 from Ernst Mayr to J. B. S. Haldane (No. HUGFP 74.7, BOX 11, F 852; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

many original ideas. His 1957 paper on the cost of natural selection is another documentation of his originality.⁸⁰

J. B. S. Haldane died in Bhubaneswar on 1 December 1964. It will please readers of this journal to know that Mayr wrote the following words to Helen Spurway 4 years later, on February 14, 1968: “I am so glad you are looking after the Haldane papers. There is a rapidly increasing interest in the history of recent biology...We just founded a new *Journal for the History of Biology*...”⁸¹

Later Assessments

The beanbag genetics controversy has not died down – an indication that the dispute had as much to do with semantics as with differences concerning assumptions or inferences, just as Lerner thought.⁸² The mathematical geneticist W. J. Ewens delivered a lecture entitled “Beanbag Genetics and After” on the occasion of birth centenary of J. B. S. Haldane at Calcutta in 1992 (in it he mistakenly dates the birth of the term ‘bean bag genetics’ to 1963). Ewens agreed with Mayr and felt that Haldane had responded to a non-issue, Mayr’s main point being quite different. He gave a number of technical reasons for saying why the assumptions made by Haldane were wrong and implied that Haldane’s attempt to defend beanbag genetics was a failure,⁸³ going so far as to refer to *The Cost of Natural Selection*⁸⁴ and *More Precise Expressions For the Cost of Natural Selection*⁸⁵ as the ‘two most unfortunate papers ever written’ by Haldane.

Ironically, Mayr had overcome his earlier reservations regarding the first of those papers sufficiently to express strong appreciation when he wrote to Helen Spurway during Haldane’s final illness (compare letters of early 1961, footnotes 44–48, and letter of 1964, footnote 80). However, Mayr is also said to have been ecstatic when he learnt of Ewens’s

⁸⁰ Letter dated 21 October 1964 from Ernst Mayr to Helen Spurway (No. HUGFP 74.7, BOX 11, F 852; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁸¹ Letter dated 14 February 1968 from Ernst Mayr to Helen Spurway (No. HUGFP 74.7, BOX 15, F 956; Pusey Library, Harvard University Archives, Cambridge, MA, USA).

⁸² Lerner, 1954.

⁸³ Ewens, 1993.

⁸⁴ Haldane, 1957.

⁸⁵ Haldane, 1961.

criticism: “For Mayr, the theoretical population geneticists were finally coming around to his perspective although this was hardly what Ewens had intended.”⁸⁶ To make matters more puzzling, Mayr changed tack once again in a favourable review that he wrote of a re-publication of Haldane’s 1932 classic *The causes of evolution*: “Haldane realised that it could lead to deceiving conclusions if one looked at each gene in isolation, because this would fail to reveal synergistic and epistatic interactions.”⁸⁷ As with Mayr’s change of opinion with regard to Wright’s contributions to evolutionary theory, it is not obvious whether this vacillation too should be attributed to an insufficient acquaintance with the literature, or to a lack of confidence in his original stand. Provine⁸⁸ discusses the point; Crow⁸⁹ hints at the first of the above two explanations in his appraisal of the beanbag genetics dispute: “Mayr was, however, criticising textbook simplifications, rather than the actual work of the three pioneers.” Or, as Smocovitis writes⁹⁰ in a review of Mayr’s last book, is it that he couldn’t quite come to grips with Haldane who, unlike Fisher, did not feel called upon to remain constrained to a single, ‘dominant’ view of evolution (“...wasn’t ever quite sure what [to] do with the overly polymathic Haldane”)?

Walter Bock (personal communication to V. R., 16 May 2006) feels that the misunderstanding arose because population geneticists had made use of genes

that were completely dominant or recessive, had little to no environmental input into the development of the phenotype, and no interaction with other genes in producing the phenotype or in the selective value of the gene. They failed to realise that the genes they used had these characteristics and that not all genes had such characteristics.

The gloomiest possible appraisal of population genetics must be that of Provine, as given in the Afterword to the re-issue of his history of the field: “Now I see these theoretical models of the early 1930s, still widely used today, as an impediment to understanding evolutionary biology...” This negative assessment extended to the evolutionary synthesis itself, which in his later opinion of 2001 was a “systematic diminution of the factors in evolution, ...[an] evolutionary constriction.”⁹¹ In contrast,

⁸⁶ Sarkar, 2005.

⁸⁷ Mayr, 1992.

⁸⁸ Provine, 2004.

⁸⁹ Crow, 2009.

⁹⁰ Smocovitis, 2005.

⁹¹ Provine, 1971 and 2001, p. 203.

just 3 years before, in the 1998 paperback edition of *The Evolutionary Synthesis*, Provine had called it “unquestionably an event of first-rank importance in the history of biology” and thought it was “more basic to the rise of modern biology” than “the revolution in molecular biology or socio-biology.”⁹²

Not surprisingly, Kimura’s view⁹³ supported Haldane:

Haldane’s works up to this stage are summarized in his book *The Causes of Evolution*, published in 1932, and together with contributions made R. A. Fisher (1930) and S. Wright (1931) in this period, may be truly called classical. Despite the simplifying assumptions they contain, they should be the basis for any future development in the theory of population and evolutionary genetics. No serious student in the field can work successfully without studying them. It is regrettable therefore, that in recent years, a tendency has developed, especially in the United States, among the naturalistic workers on evolution to deprecate these classical works as ‘bean bag genetics,’ without supplying adequate models for quantitative treatments. As mathematical education becomes widespread among biology students, it is hoped that these classical works will receive greater appreciation.

Lewontin’s writings over the years deserve special attention for their nuanced comments on the place of mathematics in evolutionary biology. He said in 1974 that population genetics had “contributed little to our understanding of speciation and nothing to our understanding of extinction.”⁹⁴ This state of affairs was attributed to (among various reasons) a lack of sufficiently accurate measurements of the parameters that went into the theory, and the ignoring of interactions between genes at different loci. More generally, he said, the problem was “the banishing of history”⁹⁵ – meaning a preoccupation, on the whole, with equilibrium rather than change (though to say so without many qualifications would be clearly unfair in the case of Haldane). A more positive assessment is found in his essay *Theoretical Population Genetics in the Evolutionary Synthesis*,⁹⁶ which contains fascinating exchanges with Dobzhansky and Mayr. Lewontin alludes to Dobzhansky’s own

⁹² Mayr and Provine, 1980 and 1998, p. 392.

⁹³ Kimura, 1968b, p. 135.

⁹⁴ Lewontin, 1974, p. 12.

⁹⁵ *Ibid.*, pp. 267–271.

⁹⁶ Lewontin, in Mayr and Provine, 1980 and 1998.

example to show how “theoretical work can directly inform experimental work” and reminds him that the relevant theory depended essentially on the inputs of Wright. He expands on “the use of all of this mathematical theory” as being an attempt to construct the logical relations that arise from various assumptions about the world. “It is an ‘as if’ set of conditional statements.”⁹⁷ To Mayr’s assertion that “for the purposes of the evolutionary biologists these very advanced theoretical analyses were superfluous,” Lewontin’s response is unequivocal: “I really disagree....We can use the products of the mathematical machinery to help us decide whether our experiments tell us what we want to know...”⁹⁸

De Winter thinks that the origin of the beanbag dispute can be traced to a “misinterpretation of the conceptual foundations” of population genetics theory on the part of Mayr, in particular of the theory as formulated by Fisher. One aspect of the misinterpretation was that Mayr took a term used by Fisher, namely “average effect,” too literally. Fisher meant that in order to compute the effect of an allele on fitness, one had to examine the consequences of the allele’s presence in all possible genetic backgrounds. According to De Winter, instead of that, Mayr took Fisher to mean that an allele always had the same effect, the “average effect.” Mayr confused an “underlying quantum theory of genic inheritance with a presumed functional quantum theory of genic interaction.”⁹⁹ Wright had made the same point much earlier in different words.¹⁰⁰ While supporting Haldane, Borges too draws attention to how Mayr’s criticisms were off the mark.¹⁰¹

Crow praises the contributions of the beanbag geneticists in an article titled “The beanbag lives on” and comments: “Gene pool models are indeed simplified.” Using the economist Herbert Simon’s words, he goes onto add, “...this is ‘meaningful simplicity’ that sweeps away ‘disorderly complexity.’ Often it is such a simplified view that provides the most useful insights into evolutionary processes ...especially dynamic aspects.”¹⁰² Whether significant advances have followed the initial attempts and the initial successes of population genetics is another issue altogether.

⁹⁷ *Ibid.*, pp. 64–65.

⁹⁸ *Ibid.*, pp. 67–68.

⁹⁹ De Winter, 1997.

¹⁰⁰ Wright, 1960.

¹⁰¹ Borges, 2008.

¹⁰² Crow, 2001.

Backdrops

While the different views on population genetics were being aired, significant changes were occurring in biology, the most momentous being the molecular revolution. The rise of molecular biology was a major backdrop to the beanbag genetics dispute, as was a continuing (and still unresolved) debate on the role of mathematics in biology. We offer brief comments on both.

The growing prestige of molecular biology and the sense of confidence among its practitioners had become contentious issues (for other biologists) by the late 1950s; the degree of self-confidence has been referred to as “imperialistic zeal.”¹⁰³ Evolutionary biologists took strong objection to the extreme reductionism espoused by molecular biologists and to what was perceived as the implied threat to the existence of their own fields: “As research in molecular biology and biochemistry intensified, the links between physicists and chemists and biologists solidified further. With the articulation and refinement of the molecular basis for genetic change, biology faced its greatest threat of complete engulfment by the physical sciences.”¹⁰⁴ Vigorous counterattacks were mounted in response, with Mayr, Dobzhansky and Simpson, all prominent architects of the evolutionary synthesis, sounding warning notes. In the same address in which he initiated the beanbag genetics dispute,¹⁰⁵ Mayr, after saying “We live in an age that places great value on molecular biology,” balanced it with “The very survival of man on this globe may depend on a correct understanding of evolutionary forces.” Dobzhansky put it thus: “In molecular biology, one spectacular discovery has followed closely on the heels of another. Molecular biology has become a glamor field...Glamor and brilliance generate enthusiasm and optimism; they may also dazzle and blindfold.”¹⁰⁶ The complexity of living systems, their hierarchical organisation and historical antecedents were invoked; a distinction between ultimate (=evolutionary) and proximate (=physiological, molecular-biological) explanations was drawn. Even so, Mayr did not hesitate to make use of the findings of Jacob and Monod to buttress his campaign.¹⁰⁷ His 1970 book¹⁰⁸ contained the words: “The day will come

¹⁰³ Dietrich, 1998.

¹⁰⁴ Smocovitis, 1992.

¹⁰⁵ Mayr, 1959.

¹⁰⁶ Dobzhansky, 1964.

¹⁰⁷ Mayr, 1963; also see footnote 79.

¹⁰⁸ Mayr, 1970, p. 183.

when much of population genetics will have to be rewritten in terms of the interaction between regulator and structural genes. This will be one more nail in the coffin of beanbag genetics. It will lead to a strong reinforcement of the concept that the genotype of the individual is a whole and that the genes of a gene pool form a unit.”

Matters came to a head when the methods of biochemistry and molecular biology were used to analyse DNA and protein sequences and draw inferences regarding phylogeny and rates of evolution. There was even talk of non-Darwinian evolution.¹⁰⁹ Some of the conclusions appeared strange, even absurd, to classically minded evolutionists. The existence of the “molecular clock” posed a major puzzle, because it seemed to imply that protein evolution went on at a constant rate that differed from one protein to another, and that it had nothing to do with evolution in the conventional sense (that is, of the organisms that housed the proteins). It took time before the realisation dawned that the word ‘evolution’ was indeed being used in different senses and the findings of molecular biology began to be assimilated into a broader evolutionary perspective.¹¹⁰ Admittedly, the relevant developments in protein sequencing and, more generally, ‘molecular evolution’ date from three or more years after the origin of the beanbag genetics dispute. Also, if the discovery of the double helical structure of DNA is taken as the notional date of birth of molecular biology, population genetics preceded it by at least three decades. Still, one sees a continuity in the resistance to the two views: the older view of population geneticists, that evolution can usefully be studied by examining the fate of single genes, and the newer view of molecular biologists, that the near-constant rates of change in DNA sequence are telling us something interesting about evolution (in both cases, ‘evolution’ being understood as organismal evolution).

The theme of mathematics in biology has been around for a long time and will not go away soon. It has two aspects. One concerns the utility of mathematics in biology, in this case evolutionary biology. The other, a separate issue, has to do with whether biology can acquire a theoretical underpinning in the manner of theoretical physics. On the first point, for organismal biologists, molecular biology and population genetics were working hand-in-hand: both were perceived to be dealing – simplistically – in the currency of single genes and their effects. The approaches were seen as aspects of the same naively reductionist world-view – and largely incomprehensible. As for the use of mathematics as such, their attitudes could not have been more different. Haldane’s

¹⁰⁹ King and Jukes, 1969.

¹¹⁰ Dietrich, 1998.

belief was that “an ounce of algebra is worth a ton of verbal argument;”¹¹¹ indeed his book had ended with the forecast: “The permeation of biology by mathematics is only beginning...the investigations here summarised represent the beginning of a new branch of applied mathematics.”¹¹²

Fisher went so far as to state that a mathematical result derived by him – roughly, that fitness does not decrease – pointed to a deep analogy with a well-known physical principle, namely that entropy does not decrease. Described by him as the “fundamental theorem” of natural selection, the precise statement was that “The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.”¹¹³ Based on the analogy, Fisher claimed for his theorem a status similar to the second law of thermodynamics: “It is not a little instructive that so similar a law should hold the supreme position among the biological sciences.” Crow’s very recent opinion is unequivocal: Haldane’s *Defense of Beanbag Genetics* did not go far enough in its claims for the successes of the mathematical treatment of evolutionary problems.¹¹⁴ Mayr felt differently, to say the least. In his view¹¹⁵ “the only contribution that the mathematical theory had made was to show that evolution by natural selection could take place in the time available for it during the history of life on Earth,” to which Sarkar adds “Interestingly, this was also the question that motivated Haldane to enter evolutionary biology and this may also account for Mayr’s preference for Haldane over Fisher and Wright.”¹¹⁶

It is a different matter whether biology is likely to develop a theoretical-mathematical underpinning similar to physics. The utilitarian role of mathematics and computational modelling in biology, including evolutionary biology, is beyond question.¹¹⁷ It is equally undeniable that mathematics is useful when it comes to addressing aspects of sub-cellular biology – for example, the working of ‘molecular motors’ – or for treating phenomena such as symmetry and patterning.¹¹⁸ But when it comes to organisms and species, history plays an essential role in deciding how biological systems are put together. To a large extent this

¹¹¹ Maynard Smith, 1965.

¹¹² Haldane, 1932 and 1990, p. 215.

¹¹³ Fisher, 1930 and 1958.

¹¹⁴ Crow, 2009.

¹¹⁵ Quoted in Sarkar, 2005.

¹¹⁶ *Ibid.*

¹¹⁷ Crow, 2009.

¹¹⁸ Forgács and Newman, 2005.

is because natural selection is opportunistic. For this reason, it is open to question whether there can be a mathematics-based theoretical biology of organisms similar to theoretical physics.¹¹⁹ Building models or theorising need not mean the same thing as using mathematics. In drawing attention to this, Godfrey-Smith makes the intriguing observation that Darwin's lack of mathematical ability may have been his strength: "He does offer abstract claims...But in fact because he does not try to formalise [...] principles mathematically, he does not find himself idealising away from the formal nature of organisms very much" but retains a "focus on the empirical and the concrete."¹²⁰ A. Weismann and H. J. Muller, two prominent evolutionary theorists, made little or no use of mathematics in their writings.

Summing Up

In one sense, Mayr's attack is valid: the early models of population genetics were simplistic. In another sense he misses the point, because it all depends on what one expects of models and on one's own perspective.

As Plutynski¹²¹ explains in the course of a discussion of the relevance of theories and models in population genetics, theories do not necessarily deal with reality. How they are assessed depends on both subjective and historical aspects: "Scientific theories are supposed to be about the world. Yet, classical population genetics is a formal discipline treating not so much the world as possible worlds... Historical context and the interests of the questioner will determine what counts as an interesting and important question, and relatedly, what counts as good answer." In other words, *what* a model contains depends on *how* one approaches it. Valdecasas et al.¹²² highlight this by focussing on the pedagogical value of models, on the "characteristics that make them appropriate for learning and transmitting knowledge." The value "heavily depends...on the individual using them...even very simple models can be useful for knowledge transmission, as the mental processes of accommodation and adjustment can make the connection between the abstract and necessarily limited model and the contingent reality."

¹¹⁹ Nanjundiah, 2005. The reasoning loses some of its force if biological form can be explained other than as a product of natural selection; see Müller and Newman (eds.), 2003.

¹²⁰ Godfrey-Smith, 2009.

¹²¹ Plutynski, 2004.

¹²² Valdecasas et al., 2009.

Two examples bring out the contrasting attitudes towards abstractions. The first of them illustrates a reaction commonly experienced by anyone who has tried to get across the notion that abstractions, in particular those implicit in mathematical models, can be meaningful. It is well known that Fisher failed to get his famous paper *On the correlation between relatives on the supposition of Mendelian inheritance* published on his first attempt in 1916. Now recognised as a classic of population genetics theory, the reasons behind its initial rejection are interesting.¹²³ Both referees turned it down. The geneticist R. C. Punnett was one of them; the biometrician Karl Pearson was the other. (Fisher memorably remarked that this was the sole occasion on which the two had been in agreement.) Among the reasons he gave for rejection, Punnett commented that the paper was “too much of the order of problem that deals with weightless elephants upon frictionless surfaces....” Evidently the analogy was meant to caricature Fisher’s approach; in the process Punnett failed to notice that ‘weightless’ did away with the problem altogether. To be fair, the comment continued, “where at the same time we are largely ignorant of the other properties of the said elephants and surfaces,” but this qualification is irrelevant for our point. The astronomer A. S. Eddington showed the opposite attitude when he used a similar analogy to illustrate how physicists model reality – in his case the illustration was meant seriously, not as a caricature. During his celebrated Gifford Lectures,¹²⁴ Eddington posed a hypothetical examination question in physics that began with the words “An elephant slides down a grassy hillside...” He went on to explain the reason for the peculiar wording: it was “only to give an impression of realism.” Facts that were provided later, namely “The mass of the elephant is two tons” and “The slope of the hill is 60°,” enabled the student to come to grips with the problem, to “[get] down to business.”

Godfrey-Smith¹²⁵ builds on Plutynski’s reasoning with his own line of thinking. He points out that the aim of building a model is to mimic the real situation, not to replicate it, and contrasts idealisation and abstraction as key aspects of science, especially evolutionary science. Idealisation treats things as if they possess features they do not have, but – as with fiction – would be *concrete if real* (note the similarity with Lewontin’s use of “as if” mentioned earlier). In contrast, an abstraction leaves things out while retaining a literally true description. The two

¹²³ Norton and Pearson, 1976.

¹²⁴ Eddington, 1928.

¹²⁵ Godfrey-Smith, 2009.

approaches are complementary. Both can be useful for model building but both have potential pitfalls. Abstractions can be close to reality but tend to be difficult to analyse; idealisations are better susceptible to analysis but maintain a greater distance from reality; they are ‘toy models.’ When developed around the time when a new line of investigation is begun, the primary value of a model of either sort is heuristic. Upon exploration the model may show that a particular line of attack bears promise – or, on the other hand, may look plausible initially but turn out to be not worth investigating further. Glymour¹²⁶ echoes Lerner’s old qualm¹²⁷ when he says that population genetics models “are, on their own, inadequate to convey an understanding of selection,” in part because they ignore the processes through which phenotypes emerge during development: “The consequences of selection do not depend on the causal details by which fitness differences arise.”

To expect that population genetics models should have addressed the problem of many interacting genes, genotype–environment interactions and their consequences for the phenotype and therefore fitness, would have been a tall order 50 years ago. Even today, that problem is reckoned to be analytically intractable and computationally forbidding. It did not help matters that with regard to what were the important questions, biologists who dealt with entire organisms saw things differently from population geneticists. For the latter, a central issue in evolution, also one that could be modelled, was adaptation. This is why their focus was on gene frequencies, genetic variation and selection within populations. For organismal biologists such as Mayr, the title of Darwin’s book encapsulated the essence of what evolution was all about – the origin of species. On this issue Mayr’s complaint about Haldane was on the mark, at least partly: “...like Darwin, he was much more concerned with showing that species are related to each other and that one can derive one species from another, than to show how this occurs.”¹²⁸ Haldane acknowledged as much, and when it came to the use of his models for quantitative genetics, more: “...both Wright’s work and my own may seem a little academic to earnest breeders of hogs or hops.”¹²⁹ Mayr highlighted features in the early population genetics models that would, ipso facto, make it impossible to tackle major issues concerning evolution, such as speciation. This was hardly news to the people who built the models. But the complaint was based on what he

¹²⁶ Glymour, 2006.

¹²⁷ Lerner, 1954.

¹²⁸ Mayr, 1992.

¹²⁹ Haldane, 1963.

thought ought to have been done, not on what had been done (though, as we have seen, he did not set much value on that either).

Controversy in science sometimes generates publicity, arguments that proceed from different assumptions and tension between the concerned scientists. Rarely has a major dispute gone hand in hand with a friendly personal relationship between the protagonists. The Beanbag Genetics dispute is one that comes under such a category. According to Provine,¹³⁰ Mayr confessed that he provided the provocation in order to stimulate further scientific work in the area. Haldane comes across as a non-dogmatic person, ready to engage in debate.

Ernst Mayr wrote to one of us some months before his death on 3 January 2005:

Prof. Haldane was a dear friend of mine. I greatly admired him and I thought he was the most brilliant person I met in my whole life...We had very much the same concept of evolution which is why we became such good friends...I am a naturalist and in Orissa I got up at five o'clock in the morning and wandered through the countryside watching birds and other animals and watching the natives as they came out of their villages to tend their fields...Haldane was quite angry that I hadn't taken him along and joined me next morning at five o'clock. I was amazed how interested he was in the animal life and all sorts of other aspects of nature. Haldane was a very lovable person in his modesty and common sense. It was a great loss that he died so relatively young.

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¹³⁰ Provine, 2004.

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