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INSIGHTS INTO THE HISTORY OF  
EVOLUTIONARY STUDIES, 1900–1970

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## CHAPTER 3

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# J. B. S. HALDANE, HOLISM, AND SYNTHESIS IN EVOLUTION

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John Burdon Sanderson Haldane (1892–1964), one of the leading biologists engaged in early genetics research, remains an anomaly. Forty-five years after his death, Haldane (also referred to herein by his initials, J. B. S.) still is the least studied of the four principal mathematical population geneticists of the evolutionary synthesis.<sup>1</sup> Beyond his biographers, few scholars offer more than a passing nod to Haldane’s research or his influence upon others.<sup>2</sup> Most frustrating, individual pieces of his work normally are studied in isolation, without reference to the comprehensive whole of this remarkably complex thinker.

Everyone struggles with Haldane. The lack of easy handles certainly has a role in this struggle. So too do his many changes in position on fundamental issues. At times, Haldane was an idealist; at other times, a materialist. For a considerable time he was a Marxist, yet this seemingly overlapped with an increasing interest in Hinduism. Haldane also presented different identities to different audiences. Notably, he often restricted philosophical comments and speculations to popular and mass audience writings.<sup>3</sup> A scholar reading his technical publications has only a partial view of Haldane no matter how thorough his or her examination might be.

Another source of confusion about Haldane involves his commitment to holism.<sup>4</sup> This point is key. Haldane’s commitment to holism was a key motivation in his research and intellectual activity, as I argue in this paper. It also motivated his interest in synthesis, both in evolution and in other realms of biology. Throughout his various shifts in philosophical position, Haldane remained committed to the principle of holism. Holism proved particularly key for Haldane during the late 1920s and early 1930s, when he struggled to embed genetics within a broader vision of evolution and then within a broader vision of biology. Haldane’s motivations might have been unique among advocates of synthesis in evolutionary studies. Nevertheless, his participation

added important momentum and material to a growing convergence of interest, the set of “common problems” so fundamental to the new generation of research in this area (Cain, 1993).

Haldane’s commitment to synthesis in evolution forms only part of a much wider ranging commitment to synthesis within his science and his world outlook in general. This theme often is overlooked or belittled. Some scholars commenting on Haldane’s science make passing reference to Haldane’s preference for a multidisciplinary approach or multifarious interests. Only two have attempted analysis in any depth (Sarkar, 1992b; Shapiro, 1993). Bartlett (1968, pp. 208–209) comes near to an explicit statement of Haldane’s antireductionism.<sup>5</sup> Even Sheehan and Graham, who correctly emphasize the importance of philosophical motivations in Haldane’s science, have not examined the connections between Haldane’s philosophy and science in depth and detail (Graham, 1973, p. 264; Sheehan, 1985, pp. 316–326). Yet the question of how Haldane’s philosophy and science interacted needs to be seriously addressed before we reach a solid understanding of Haldane and his work. This paper is an attempt to give a broad outline to such a project.

This paper follows Haldane through the first three decades of his career, from his physiological work in the early 1920s and through his biochemical research and interest in population genetics during the interwar years. It also offers a brief section on Haldane’s uptake of dialectical materialism, the Marxist holistic philosophy, noting his use of it in the 1930s. Finally, it presents a few examples from Haldane’s post-World War II work to show continuity in his holistic outlook. To begin, I describe some key features shaping Haldane’s philosophical framework.

### HALDANE’S PHILOSOPHICAL COMMITMENTS

Haldane’s philosophical commitments changed during his lifetime. One theme in those commitments involved a move from idealism to materialism. Another grew out of his frustration with the tension between mechanism and purpose in biology.

While an adolescent, J. B. S. was heavily influenced by his father, John Scott Haldane (Clark, 1968, pp. 17–19, 26–30; Werskey, 1988 [1978], pp. 53–60). J. S. Haldane (referred to herein as J. S. to distinguish father from son—J. B. S.) was a physiologist who promoted the application of neo-idealistic and antireductionist principles to biology, drawing from Kant and especially Hegel (Sturdy, 1988). However, as J. B. S. gained broader experiences, his commitments shifted in important ways.

J. B. S.’s participation in the Great War (World War I) challenged his neo-idealist preconceptions and showed the need for something better grounded in experience. After witnessing a massacre of allied troops in 1915, for instance, J. B. S. reflected on Hegel’s conclusion that “the real is the rational.” This, J. B. S. suggested, “appeared to me to be refuted by the existing circumstances” (Haldane c. 1942, p. 14). Shortly after the war, J. B. S. also recalled developing serious doubts over the validity of Hegel’s “political tenets” (Haldane, 1995 [1923], p. 27). These doubts ebbed and flowed over the next decade. In the early 1920s, J. B. S. confidently predicted “Kantian idealism” would replace “materialism” as the “basal working hypothesis” for all human activities, beginning with science (Haldane, 1995 [1923], p. 27). By 1930, or around that time, J. B. S. referred to himself as “agnostic” regarding which side was correct,

though he admitted being “much attracted to a modified Hegelian view” (Haldane, 1937b [1932], p. 169).

Importantly, Haldane also had developed some sympathy for materialism by 1930.<sup>6</sup> In 1923 he had accepted a senior post in biochemistry at the Dunn Laboratory, University of Cambridge. The head of the laboratory, the biochemist Frederick Gowland Hopkins, encouraged his staff to discuss the philosophical implications of biology, with his own brand of holistic materialism often being enthusiastically adopted by his fellow biochemists. An important component in these discussions was the still ongoing debate among both philosophers and philosophically inclined scientists as to the implications of the “new physics” (i.e., quantum mechanics and relativity theory) for philosophy and science. Haldane showed a keen interest in both Hopkins’s materialism and its implications for biological research, and the new physics debate. This was also the period in which Haldane studied dialectical materialism, the Marxist holistic philosophy. Haldane synthesized these influences to create a materialist philosophical position in the early 1930s, certainly no later than 1933.<sup>7</sup> He kept this position at least until 1950, when he left the Communist Party of Great Britain.

Haldane’s views after 1950 are as poorly understood as are his views prior to 1950. Several historians claim that, after his move to India in 1957, Haldane increasingly embraced Hinduism (Clark, 1968, p. 207; Dronamraju, 1985, pp. 8–9; Sarkar, 1992b, pp. 404–405). At the same time, other evidence suggests Haldane still considered himself primarily a Marxist.<sup>8</sup> More study is needed to understand how these views coexisted in Haldane’s overall commitments.

Throughout these struggles with idealism and materialism, Haldane remained a holist. His interest in the relationship between mechanism and purpose, and his struggle to find a solution to the debate between mechanists and vitalists, illustrates his approach.

As has been well studied, neo-idealism in the late nineteenth century arose in response to ardent materialism of previous decades. This in turn provoked a materialist response remembered thereafter (at least in biology) as a debate between mechanists and vitalists.<sup>9</sup> Both sides equated mechanism with materialism, especially as mechanism related to physicochemical methods and explanations.

Vitalism was associated with idealism. Advocates included the embryologist Hans Driesch, the proponent of creative evolution Henri Bergson, the naturalist E. S. Russell, and J. B. S.’s father, J. S. Haldane. Idealistic vitalists stressed the importance of purposive activity within organisms (e.g., self-regulation, regeneration of lost limbs, and embryonic development). They argued purposive activity constituted a distinct kind of biological activity, one that could not be understood through an examination of component parts and processes at all. Such investigations can only access physicochemical manifestations of purposive activity. For J. S. Haldane, these parts were subordinate to the intact organism functioning as a biological whole. Purpose had primacy.<sup>10</sup>

Mechanists emphasized the predictive success of physicochemical laws within biology. When they failed to account for features of complex systems, mechanists argued their laws should be supplemented or modified, rather than abandoned for an alternative metaphysics (Anonymous, 1906, 1914a, 1914b, 1916; E. H. S., 1917; Hardy, 1906).

When J. B. S. engaged the subject after the Great War, he took the view that both sides of this debate each had positive value, as well as valid criticisms. Still, a more encompassing solution was needed (and he was not alone in this conclusion).<sup>11</sup>

Agreeing with mechanists (or materialists), Haldane argued, it came as no surprise that every process in living organisms obeyed the laws of physics and chemistry. On the other hand, and agreeing with idealistic vitalists, “these processes are coordinated in a way characteristic of the living organism. Thus, we cannot avoid speaking of the function of the heart, as well as its mechanism” (Haldane, 1932e [1927], p. 127). Neither side of this question deserved primacy, Haldane stressed, because the real question should be about their relationship (Haldane, 1932e [1927], pp. 127–129). Appealing to Kant, Haldane suggested mechanism and purpose might “cohere in one principle”—what Kant called “synthesis.” Even though “our reason cannot so unite them” now, he held out hope this would occur in the future (Haldane, 1932e [1927], p. 128). Haldane’s desire for synthesis separated him from his father, who insisted on the primacy of purpose.

### WHOLE ORGANISMS AND HOLISTIC PHYSIOLOGY

J. B. S.’s holism appeared in his first research, which involved experimental physiology. Accepting a fellowship at New College, Oxford in 1919, Haldane began teaching physiology. Respiration was the only part of the subject he knew well, so a crash course from his father kept J. B. S. ahead of his students (Pirie, 1966, p. 220). While in this position, J. B. S.’s scientific research was predominantly in physiology with occasional excursions into genetics.<sup>12</sup>

In the 1920s, J. B. S.’s physiological research followed in his father’s footsteps. J. S. started with an idealist epistemology, whereby causal relationships between physical and chemical observations are not the only causal relations that can be inferred legitimately from scientific research. Of particular importance was J. S.’s idealist inference that a distinctive property of biological phenomena was a teleological coordination maintaining the normal functioning of the organism as a whole.

In experimental practice, J. S. focused on activities of whole, intact organisms. His work typically involved examining the rate at which whole organisms exchanged energy and substances with their environment. These exchanges were understood to be manifestations of the purposive activity of the organism in maintaining itself. The “laboratory” could be any location where J. S. could recreate living conditions that organisms might naturally encounter (Sturdy, 1987, pp. 201–220).

J. B. S. adopted J. S.’s research and epistemology (Clark, 1968, pp. 59–62, 135–151). He studied organisms as intact wholes. He avoided severe disruption to the subject. His laboratory could be almost anywhere. He also regularly turned himself, and his research associates, into experimental subjects. Indeed, Joseph Needham’s earliest recollection of J. B. S. involved finding him staggering at the stairs to the biochemistry department in the University of Cambridge. Haldane had been performing a physiological experiment on himself in which he was trying to ascertain the maximum safe dose of sodium bicarbonate (Mourant, 1968, pp. 319–320).

Although Haldane used a holistic method derived from his father’s application of neo-idealism to physiology, J. B. S. was not in full agreement with his father’s emphasis on purpose. J. B. S. also wanted to balance this with a place for mechanism (i.e., physicochemical pathways). Only the combination could lead him to a nonreductive cohering principle and produce the Kantian synthesis he desired.

### THE INFLUENCE OF HOPKINS'S HOLISTIC BIOCHEMISTRY

In 1923 Haldane left Oxford to become the first Sir William Dunn Reader in Biochemistry at the University of Cambridge. It was here that Haldane encountered the philosophical and biochemical approach of Frederick Gowland Hopkins. This had a profound influence on Haldane.

Haldane's Readership might seem unexpected given his training in physiology and not chemistry (Werskey, 1988 [1978], pp. 82–83). The explanation lies partly in the fact that biochemistry was not yet a separate discipline from physiology (Clark, 1968, p. 63). More directly, Haldane had abilities that would have appealed to Hopkins, and Hopkins made the key recruiting decision. From the reverse perspective, Cambridge had a strong appeal for Haldane. Hopkins wanted biochemistry to study not only reactions in the whole body (rather than just the isolation and identification of chemical products) but also exact laws governing biological molecules. It also should produce increasingly exact experimental methods, and its exponents should have an interdisciplinary training. From his vantage point, Haldane could hardly find a more suitable environment. His physiological research met Hopkins's first three aims; his broader interest in biology met the fourth (Sarkar, 1992a, pp. 56–60).

Haldane enthusiastically adopted Hopkins's approach (Haldane: 1932c [1927], c. 1933). Central were Hopkins's concepts of dynamic equilibrium and levels of organization. In dynamic equilibrium, the organism persistently maintains itself against its external environment through the coordination of chemical reactions (particularly by the use of enzymes) and the distribution of necessary chemicals throughout the body.

A closely associated idea involved levels of organization. Levels included, for example, individual cells, organs, and whole metazoan organisms. While holding properties in common with a lower level, entities at a higher level also exhibited additional properties characteristic of that higher level. For Hopkins this was not simply an aggregation of properties whilst ascending the levels. The properties or behavior of entities at lower levels were affected in part by those at higher levels. So he studied the interaction of properties at different levels. For example, Hopkins stressed the importance of chemical coordination (organs coordinate cells; cells coordinate molecules). This kind of organization "illustrates that subservience of parts to the whole which characterises an organism" (Hopkins, 1932a, p. 870). Likewise in metazoans, "the cell has esoteric qualities which may call for *organising influence of a greatly different kind, exerted maybe at some higher level*" (Hopkins, 1932b, p. 16, my emphasis).<sup>13</sup>

Hopkins's approach had philosophical appeal for Haldane in the 1920s. In the mechanism-vitalism debate, for instance, Haldane was unhappy with the solutions proposed for the relationship between mechanism and purpose, and he sought a cohering principle. For Hopkins, levels of organization interacted such that wholes and parts partially determined the properties of each other. Though deliberately materialistic, this made purposive activity a property of whole organisms, and it meant that purpose could be determined both by certain physicochemical properties specific to whole organisms (e.g., self-maintenance) and by physicochemical interactions of the parts within the whole. This process-based antireductionism did not subsume purpose to mechanism, nor vice versa.

Also important for Haldane, Hopkins's vision was not limited to the biological domain. Hopkins incorporated aspects of the work of philosopher Alfred North

Whitehead into his scheme. In the 1920s Whitehead argued the new ideas in quantum mechanics demonstrated that all entities, both the living and the nonliving, were self-sustaining systems. In this sense, every entity could be understood as “organic”—physical entities exhibiting a form of self-regulation or self-maintenance. For Whitehead, this extended a biological concept into physics. For Hopkins, it offered a way to extend notions of levels of organization and dynamic equilibrium to much broader domains. Such a sweeping holistic vision certainly appealed to Haldane.<sup>14</sup>

Until now I have concentrated on the philosophical abstractions that Haldane would have found attractive in Hopkins’s biochemical vision. But it should be remembered that Haldane learned his research techniques in biochemistry through the lens of Hopkins’s dynamic approach. Theory and practice would have acted to reinforce each other in Haldane’s eyes. A significant portion of his practical work entailed what became known as biochemical genetics.

Part of this work focused on the relationship between genes and enzymes. Haldane began this interest several years before his introduction to Hopkins’s philosophy of biology, but his approach significantly changed after his move to Cambridge. From 1920 to 1927 the basis of Haldane’s work on the gene-enzyme relationship was that multiple alleles of a gene produced differing quantities of the same enzyme (and therefore differing intensities of the same trait) (Haldane, 1920, p. 10; 1922; 1927c). Thus, Haldane concluded, the relationship between alleles and enzymes was one of mechanistic aggregation of quantity.

It would be a mistake to assert that this conclusion marked Haldane as a mechanical reductionist. During this period, Haldane took a proximate compromise familiar to many other geneticists, including T. H. Morgan and A. H. Sturtevant (Allen, 1978). Because so little was known about the nature of genes, it was necessary to treat them mechanistically until more basic information was collected (Haldane, 1927d, p. 456). (Also, this compromise would not have been a problem for the neo-Kantian Haldane of the mid-1920s, for whom mechanism could be useful in biology even though alone it was not sufficient.<sup>15</sup>) At the same time, Haldane kept a broader holistic vision as his ultimate goal. While chemical processes could be “taken one at a time . . . [and could] often be imitated by artificial means,” nonetheless “what is characteristic of life is not the individual details of structure or behaviour, but the way in which *they cohere to form a self-regulating and self-preserving whole*” (Haldane, 1932b [1927], p. 45, my emphasis).

Interestingly, Haldane added a qualitative conception of allelomorphic series in an unpublished paper written around 1931. While in some cases a quantitative conception explained the data, in other cases “a series of multiple allelomorphs produce a series of different but closely related enzymes” (Haldane, c. 1931a, p. f 47). These created “qualitatively different specific substances” (Haldane, 1931a, p. f 65). In this case, the mechanistic side of Haldane’s theory of the gene gave way to a more dynamic, interacting process.

This shift was not trivial. In 1927, Haldane had an atomistic focus on the gene; in particular, a focus on gene products and the gene’s relation to a specific identifiable trait. By about 1931, he had shifted to classifying genes according to the biochemical functions they performed. In this case genes became part of more complex and dynamic developmental processes.<sup>16</sup> This shift is evidenced further in Haldane’s claim that various authors showed “that a gene may alter the amount of an enzyme in a tissue, or at least the activity of the enzyme there found. But the amount of enzyme



*may also vary rapidly through nongenetic causes*" (Haldane, 1931a, p. f43, my emphasis). Notably, "nongenetic causes" and "individual details" were not subsidiary agents compared with genes. This was a holist's view.

One of the most important markers in Haldane's more holistic approach to biochemistry was his essay, "The Time of Action of Genes" (Haldane, 1932g). This attempted an ambitious synthesis of genetics, biochemistry, and embryology.<sup>17</sup> As he did the year before, Haldane classified genes by their function, not their end product or trait. He also classified genes according to their time of action within the developing organism (sometimes even with other organisms [Haldane, 1932g, p. 6]). Using this approach, Haldane speculated on how the interplay between enzyme, gene, and environment affected developing organisms, and how changes in this interplay contributed to evolutionary change. For example, Haldane referred to the growing tadpole absorbing proportionately more water than salts from its environment. Thereafter, the concentration of salts within the tadpole decreases, and this affects enzyme activity (Haldane, 1932g, p. 20). According to Haldane, "This process will affect a whole group of enzymes (e.g., amylase, fumarase, and catalase) and have very little effect on others. Thus, a change in permeability [affecting water absorption] due to a single gene would affect the time of action of many others" (Haldane, 1932g, p. 20). Since each enzyme may be used in "several quite separate processes," a change to one gene can accelerate or retard the time of action of a whole group of enzymes (Haldane, 1932g, p. 20). Natural selection of such a gene could therefore result in several marked evolutionary changes in an organism.

Again, this discussion could be construed as part of a reductionistic argument for genetic control of organisms. However, within the context of Haldane's holism, such biochemical explanations required context; for example, the demands on organisms related to environmental constraints and consequently the timing of gene action. Also, for Haldane, a gene would only constitute one detail within the biological whole. So "a change to one gene" would mean a change to one detail within the whole that happens to have a marked effect upon the whole (just as, in a similar manner as seen above, an enzyme could also be a detail producing a marked change in the whole).

In a series of lectures delivered in 1940, Haldane continued this approach to classifying genes by function and process rather than by a correlated trait. He now classified genes "by their chemical effect" (Haldane, 1941, p. 72) and spoke of the gene as "responsible for a unit process [for example, acidity, rather] than for a unit character" (Haldane, 1941, p. 21). He argued that functions of the genes were analogous to organ functions, leading to the strongly holistic claim, "We can regard the gene as an organ in the cell, just as the heart, pancreas, or femur is an organ in the body as a whole. *Now in the last analysis the function of an organ depends on the other organs and the environment*" (Haldane, 1941, p. 22, my emphasis).<sup>18</sup>

To summarize, Haldane's scientific practice changed in the 1920s and early 1930s as he appropriated Hopkins's conceptions of dynamic equilibrium and levels of organizations. These introduced Haldane to a different form of materialist philosophy and practice than the mechanistic variety he had previously considered. Its appeal was undoubtedly due, in part, to its potential for a unified picture of the world and its potential to unify biological disciplines in the sense of an intellectual, nonreductive synthesis. This can be seen in Haldane's attempts at a synthesis of genetics with biochemistry. Even more striking was his synthesis of genetics, biochemistry, and embryology in "The Time of

Action of Genes" (1932g). Finally, Haldane used a mechanistic approach in the 1920s to consider the relationship between gene and enzyme. By his own admission, this was a limited, temporary approach. He discarded it in 1931 for a more holistic one. As will be seen, Haldane also used this compromise in later genetic work. Its provisional nature proves crucial to understanding Haldane as a geneticist.

### POPULATION GENETICS AS A SYNTHESIS OF GENETIC AND ECOLOGICAL MECHANISMS

As with his biochemical work, Haldane's other genetics research moved from a mechanistic to a holistic context. The sequence of events and chronology were similar, with the transition around 1930 and with genetics playing a cooperative role in his synthesis for "Time of Action" (1932g). In this section, I examine Haldane's early, predominantly mechanistic, approach to population genetics. This is followed by an examination of his synthesis of certain genetic mechanisms with ecological mechanisms in 1930 and the place of this development in his article two years later, "Time of Action." This section ends with a comparison of Haldane's approach with Sewall Wright and R. A. Fisher, then comments on Ernst Mayr's accusation that Haldane's genetic work was merely "beanbag genetics."

During the 1920s and 1930s Haldane gradually built up a body of work in population genetics (Clark, 1968, pp. 29–31; Mitchison, 1968, p. 303; Pirie, 1966, p. 220; Werskey, 1988 [1978], pp. 57–58). Hailing from the Darwinist tradition at Oxford (Mayr, 1998 [1980], p. 11) and with a flair for mathematics, Haldane declared that the way forward for the Darwinist cause was to add mathematical rigor to Darwinian evolutionary theory (i.e., to use quantitative arguments in favor of natural selection as an explanation for evolution, rather than rely on purely descriptive arguments) (Haldane, 1924a, p. 19). To this end, he began in 1924 a series of papers, "A Mathematical Theory of Natural and Artificial Selection." In this series he devised mathematical models to examine the effect of different intensities of selection under various conditions. He began with simple conditions that finally led to a "stable equilibrium" in the genetic composition of the population (Haldane, 1924a, 1924b). This was followed by cases resulting in no equilibrium, unstable equilibrium, or oscillations of the population's genetic composition (Haldane, 1926, 1927a, 1927b).

Shapiro correctly refers to these early papers in the "Mathematical Theory" series (papers 1 to 5, 1924–1927) as having "an unremittingly reductionistic [mechanistic] emphasis in the way the models are constructed" (Shapiro, 1993, p. 74). (He is not claiming these papers were *exclusively* reductionistic in emphasis.) Shapiro does not explain what he means by this "reductionistic emphasis," but no doubt the following is his intended meaning. In each model, the population consists of a billiard ball universe of genes, or Mendelian factors. Once the conditions for the model have been obtained, the system will run in a mechanistically determined manner to its conclusion. This was as true for Haldane's models of unstable and oscillating populations as for stable ones.

The mechanistic emphasis in Haldane's early "Mathematical Theory" papers is unsurprising. This was a convenience. With very little previous work on this issue, Haldane argued, it was necessary to start with the simplest cases and then move on to the more complex (Haldane, 1924a, p. 19). As seen earlier, he made a similar compromise in his work on the gene-enzyme relationship during this time. From the

start of this series, Haldane stated his intention to use quantitative arguments in favor of natural selection as a feasible explanation for evolution, rather than rely on purely descriptive arguments.

After a gap of three years (1927–1930), Haldane returned to his “Mathematical Theory” series. In the intervening period he almost certainly met Sergei Chetverikov at the Fifth International Congress of Genetics in Berlin in 1927. Haldane was so enthusiastic about Chetverikov’s work, he apparently had the Russian works of the Chetverikov group translated into English and made available in his laboratory for his own coworkers (Adams, 1998 [1980], p. 268). Chetverikov and his group had already established a conjoining of biometrics, natural history, and genetics within a Darwinian framework (Adams, 1998 [1980], pp. 243, 262). Their synthesis of these elements was not intended to be reductionistic (Adams, 1998 [1980], pp. 246, 248, 253). No doubt Haldane’s enthusiasm stemmed partly from his own desire to synthesize these same elements into a broader framework (Haldane, 1924a, p. 19). Whether Haldane gained any philosophical insight from the group’s work remains an open question. Regardless, their scientific work surely must have had an impact on the next phase of Haldane’s developing picture of population genetics. It helps explain, for instance, the incorporation of ecology.

The next three papers in Haldane’s “Mathematical Theory” series were produced almost simultaneously in 1930.<sup>19</sup> These papers introduced a sense of internal dynamics into populations, something missing from earlier “Mathematical Theory” papers. Populations were treated as a cluster of metastable (potentially unstable) populations and semi-isolated communities. This was the first occasion these two themes appeared in Haldane’s work. They constitute the genetic and ecological mechanisms, respectively, in his developing picture of the processes of evolution. They also signal a move away from a narrowly mechanistic toward a more holistic approach—in other words, a synthesis of genetic and ecological aspects of evolution, rather than a reduction of one discipline to the other.

Regarding metastability, Haldane gave the example of a population containing genotype AABB with occasional mutations of **A** and **B** to **a** and **b**, respectively. Occasionally, a section of this population becomes temporarily isolated from the main population (Haldane, 1931c, p. 138). The genotype aabb subsequently becomes the “stable type,” that is, the majority genotype of this semi-isolated community. When this community regains contact with the main population one of three outcomes is possible. Firstly, aabb becomes “swamped by hybridisation” with AABB. Secondly, “aabb may possess or develop characters which render meeting with AABB rare.” Thirdly, a species may exhibit “metastability” due to certain genetic mechanisms. In Haldane’s example,

chromosome changes may occur to cause close linkage of A and B when the populations are crossed. Thus if the loci of A and B are in the same chromosome an inversion of the portion containing them will lead to their behaving as a single factor on crossing. In this case if  $K$  [the viability of type aabb] is positive the whole species will be transformed into the type aabb. A species which is liable to transformations [due to genetic mechanisms] of this kind may be called metastable. Possibly metastability is quite a general phenomenon, but it is only rarely that the circumstances arise which favour a change of the type considered. (Haldane, 1931c, p. 139)

So Haldane strongly suspected many species (and populations) were metastable. A change in the genetic composition of species and populations was due as much to the internal nature of the species as it was to a change in environmental conditions. In other words, the internal structure of the population (in this example, linkage possibilities) contains the potential for change. A change in the conditions (external factors) under which the population exists can allow this potential to be realized. This emphasis upon the nature of the internal differentiation of a species and its implications for evolutionary change was a distinct move away from the earlier mechanistic approach in the first five “Mathematical Theory” papers. It is worth recalling that this move toward a more systems-based, holistic model in his population genetics occurred in the same period as similar changes in Haldane’s biochemical work.<sup>20</sup>

Regarding ecological mechanisms, Haldane stated that evolutionary changes linked to metastability could only occur when “circumstances arise which favour” such a phenomenon. He suggested that these circumstances involved disturbances to a population resulting in semi-isolated communities. This phenomenon was particularly important in the evolution of higher animals (Haldane, 1932f, p. 103). In the “Mathematical Theory” papers, Haldane drew heavily on the zoologist G. P. Bidder’s notion of “cataclasm” for this ecological mechanism.<sup>21</sup> Bidder used cataclasm to denote a nearly overwhelming catastrophe striking a species or population. The peculiar spelling was meant to avoid confusion with “cataclysm,” which Bidder took to mean “a widespread submergence of land” (Bidder, 1930, p. 783). Bidder argued cataclasm disrupted a population’s environment. In such cases, characteristics that are “normally useless” may suddenly become vital to survival (Bidder, 1930, p. 783). Periodic cataclasm, even separated by long intervals, could therefore result in widespread distribution of such characteristics (Bidder, 1930, p. 783).<sup>22</sup>

Aside from the presence of useless characters for normal life, Bidder also noted two other effects of “cataclasmal selection.” First, organisms carrying cataclasmically advantageous characters may also carry over characters selected for a precataclasmic environment. Second, even “small quantitative differences may have survival value in a cataclasm” (Bidder, 1930, p. 784). From these considerations Bidder concluded that cataclasmal selection may “explain otherwise inexplicable characteristics” (such as the apparently useless ones mentioned above) (Bidder, 1930, p. 786).

In “Mathematical Theory” paper 7, Haldane introduced the idea that “the direction of selection [for certain genes] will be reversed” under certain circumstances (Haldane, 1931b, pp. 133–134). He went on to say,

This is in full accordance with the views of Bidder, who points out that, where “cataclasm” occasionally destroy the vast majority of a species, characters which are useless or worse under normal conditions may be selected. He specially mentions the case of a violent or erratic response of an animal by migration or otherwise to unfavourable environments, which would be likely to lower the average viability, but increase its dispersion. (Haldane, 1931b, p. 135)

So Bidder’s scenario offered an explanation for why a character could switch from being disadvantageous to advantageous and why the direction of selection could be reversed.<sup>23</sup> This was stated more explicitly in “Mathematical Theory” paper 8:

Almost every species is, to a first approximation, in genetic equilibrium; that is to say no very drastic changes are occurring rapidly in its composition. It is a necessary condition for equilibrium that all new genes which arise at all frequently by mutation should be disadvantageous, otherwise they will spread through the population. Now each of two or more genes may be disadvantageous, but all together may be advantageous. An example of such balance has been given by Gonsalez (1). He found that, in purple-eyed *Drosophila melanogaster*, arc wing or axillary speck (each due to a recessive gene) shortened life, but the two together lengthened it. (Haldane, 1931c, p. 137)<sup>24</sup>

If Haldane noticed disagreements with Bidder's theory, he chose not to state them (perhaps because this was a short mathematical paper). However, several differences are easily discernible. Haldane differed from Bidder in his synthesis of ecological with genetic factors. Also, where Bidder spoke of useless characters Haldane spoke of disadvantageous recurrent mutations. A cataclasmic disruption of a population could turn these mutations from being disadvantageous to advantageous to the organism. These mutations could then become the "stable type" in the semi-isolated community suffering from the cataclasm. If this type was metastable it stood a far greater chance of becoming established in the parent population when reintroduced to it.

Haldane pursued similar themes in his synthetic 1932 paper "Time of Action," where he produced further arguments for processes that could lead to the "sudden appearance" of ancestral characters, the eruption of "violent evolutionary novelties," "apparently useless evolution," or even interspecific differences and therefore speciation events (Haldane, 1932g, pp. 15–17, 20).

This is the context for comparing Haldane's work to that of Fisher and Wright. A detailed analysis is not possible here. I simply will suggest one potential starting point, focusing on the place of ecology in each of their respective schemes. Philosophically, Fisher's approach to population genetics was atomistic and strictly selectionist within panmictic populations (Hodge, 1992, pp. 247–253). Scientifically, his ecological picture was derived through his ongoing association with Edmund Brisco Ford.

Wright was a holist (Provine, 1986, p. 235) though his population genetics did not have an ecological aspect. His adaptive landscapes had the appearance of adding an ecological dimension to his theory, but they had only a limited applicability to natural populations (Provine, 1986, pp. 307–317). It was not so much his holism that constrained his vision as his science. In the early 1930s Wright was known as an animal breeder, physiological geneticist, and increasingly as a quantitative evolutionary theorist. Although he was aware of current theory in natural history and systematics this contained a bewildering number of explanations or mechanisms for variations between closely allied species (Provine, 1986, pp. 291–297; Cain, 1993, pp. 3, 17). For some reason, Wright failed to choose between them.

Haldane's population genetics differed from Fisher and Wright in that he had a holistic view *and* an ecological mechanism. In common with Wright, he thought Fisher's model had limited applicability to evolutionary processes and semi-isolated communities played an important role. Unlike Wright, Haldane had a substantive ecological mechanism, drawing on Bidder's cataclasms. Perhaps Haldane's decisive stance on an ecological mechanism was in part due to the influence of Chetverikov.

Ernst Mayr's famous dismissal of mathematical population genetics as "beanbag genetics" (Mayr, 1959) deserves special comment. Haldane's approach certainly did

not fit Mayr's representation of an overly simplistic discipline ignoring broader biological contexts. Haldane (1964) made this point, and continued to argue for a multifaceted approach to biology in which genetics played a nonreductive role. He also argued for using mathematics as a nonreductive tool for understanding biological processes.

### A HOME IN DIALECTICAL MATERIALISM

During the period of Haldane's intellectual synthesis of the early 1930s, he was also undertaking a rigorous study of dialectical materialism.<sup>25</sup> Hopkins's materialist program had helped to show Haldane that it was possible to be a materialist and a holistic scientist. Dialectical materialism gave Haldane a wider ranging set of unifying principles with which to investigate and explain the world. He was particularly excited by the possibilities of the materialist dialectic as expressed in the law of the unity of opposites (Hammond, 2004, pp. 84–91). This principle appeared to be the primary driving force behind all processes—a strong unifying principle indeed!

Haldane certainly was attempting to apply dialectical materialism to his philosophical concerns no later than 1933. In "Quantum Mechanics as a Basis for Philosophy," published in January 1934, he proposed a solution to the mind-body problem that was not just holistic but also dialectical materialist in perspective (Hammond, 2004, pp. 87–91). The scientific research implications from this model were obvious (even if not practically possible at the time).

Traces of the dialectical materialist approach in Haldane's scientific work may be found in his "Mathematical Theory" series as early as 1930 (Hammond, 2004, pp. 133–135). His first mature application to his science probably came in his mutation-selection model of 1935 (Haldane, 1935). This model led to a research program extended at least to 1940 (Haldane, 1939a; Haldane, 1939b, 1940; Haldane & Moshinsky, 1939; Hammond, 2004, pp. 115–128).<sup>26</sup> He also promoted the application of Marxist holism to science through such works as "A Dialectical Account of Evolution" (Haldane, 1937f) and *The Marxist Philosophy and the Sciences* (Haldane, 1939c).

### HALDANE'S HOLISM AFTER 1945

After 1945, Haldane's scientific output appears overwhelmingly genetic in character. Yet he was not pursuing a reductionist program. He had hoped to continue his biochemical work upon acceptance of a full-time post at University College London in 1937, and he was expected to do so. But shortly after his appointment World War II disrupted his work at the university, and in the immediate aftermath of the war facilities and funding were severely limited in Britain (Clark, 1968, pp. 93). He had to be realistic. Also, his biochemical research program had run its course. In typical Haldane fashion, he had quickly passed onto other possibilities and left remaining issues for other researchers (Darlington, 1966, p. 5; Darlington, 1968; Sarkar, 1992a, p. 75).

When Haldane spoke at the famous 1947 Princeton conference on "Genetics, Paleontology, and Evolution," he stressed the need for a holistic understanding of evolutionary processes, introducing his paper with a profound comment:

Only evil can come from forgetting that man must be considered from many angles. . . . You can treat him as a thinker, as an individual, as a member of society, as a being capable

of moral choice, as a creator and appreciator of beauty, and so on. Concentration on only one of these aspects is disastrous . . . any attempt to reduce ethics and politics to biology . . . [will result in] . . . a moral degradation [as happened in Hitler's Germany]. (Haldane, 1949b, p. 405)

This paper was a pluralistic romp through the history of humanity and its possible future. With the exception of Muller's summary to the conference, all the other authors in this conference focused narrowly on parts of the wider picture, reflecting the postwar differentiation of professional concerns.

In "Disease and Evolution" (1949a), Haldane suggested disease acted as a positive agent in evolution. Intrinsic to his argument was the group (and species) as a unit of selection. These units constituted nonreductive levels of organization. The concepts in this paper can in part be traced from previously existing elements in Haldane's intellectual makeup, including the negation of the negation from dialectical materialism (Hammond, 2004, pp. 135–140).

Haldane continued to promote a version of nonreductive levels of organization as part of an explanation for multifarious aspects of reality in "Time in Biology" (1956). To this end he classified various processes according to their timescale, acknowledging a debt to Joseph Needham's concept of "integrative levels of organization." This Needham based, at least in part, on Marxist holism (Needham, 1976 [1937]).<sup>27</sup> In this paper, Haldane also continued to insist cell constituents—for example, proteins—were not alive but merely "details" within the cell as a living whole. He linked this argument to ideas expressed by Friedrich Engels (Haldane, 1956, pp. 389–391). Haldane included DNA in this holistic list of "details."

A final example involves Haldane's attempts to distinguish living from nonliving entities. Haldane always admitted our present level of knowledge made it impossible to give a complete definition of this distinction. Still, we can make a start. In his 1930s Marxist writings, Haldane applied the concept of "quantal events" to the structure of the cell. He suggested that whole cells may have a unity similar to that found in a molecule with "a system of energy levels peculiar to the cell as a whole, just as the molecule has systems of energy levels which do not belong to any of its constituent atoms, and yet are not imposed upon it from outside" (Haldane, 1939c, p. 105).<sup>28</sup> Haldane was arguing that while there is a material continuity between the living and nonliving, there is an energy level discontinuity—a dialectically qualitative distinction between organisms and inanimate objects. It is also significant that he emphasized this qualitative distinction was not imposed upon the organism or system from outside, but was due to the nature of the entity itself (i.e., the properties arise due to the internal organization of the system or whole). He was still promoting this holistic concept in his last years (Haldane, 1963).

## CONCLUSION

Throughout his life Haldane was a holist. In his philosophical development, shifts in his position were from one holism to another. At no stage did he consider that mechanism alone could hold the key to a unified picture of biology. It was useful but not sufficient.

Haldane attempted to incorporate his specialized interests into an increasingly broader, holistic picture. This is particularly important in the early 1930s, a robust period

of intellectual synthesis for him. Haldane entered this period with an established holistic approach to physiology. In his biochemical genetics, he moved from an “atomistic” to a developmental (and holistic) approach in approximately 1931. His work in population genetics expanded from a narrowly mechanistic approach to one that included ecological aspects inspired by Bidder and almost certainly Chetverikov by 1930. In his paper “Time of Action” (1932), he attempted a synthesis involving genetics, biochemistry, and embryology. These developments were partly influenced by Haldane’s move from a hesitant support for idealistic holism to an acceptance of materialistic holism, finally in the form of dialectical materialism. Both Hopkins’s holistic materialism and dialectical materialism played a role in Haldane’s intellectual synthesis.

## NOTES

1. For all his quantitative work, Haldane should nonetheless be treated as a biologist, not a mathematician. He regarded mathematics as an important servant of biology, a tool to be used to achieve the ends of biological inquiry (Haldane, 1937d [1932]; 1956, p. 398; 1964, pp. 7–8). Note that all citations of Haldane are to the works of J. B. S. Haldane, unless indicated otherwise.
2. Principal biographical sources on Haldane are still Clark (1968), Dronamraju (1985), and Pirie (1966).
3. Even the Haldane Archives at the National Library of Scotland and University College London are not much help when studying his broader scientific or philosophical thinking. Few reflective discussions are preserved there.
4. Originally coined in 1926, holism referred to one particular style of antimechanism (Hancock, 1962, pp. 304–306; Kerr, 1927). This original use was rejected by Haldane, among others (Haldane, 1937c [1932], p. 246; Needham, 1931, pp. 30–32). For a study of its different uses by historians see Lawrence and Weisz (1998). Broadly construed, holism is a species of antireductionism that insists the whole is greater, in some sense, than the sum of its parts. Here, I use the term in its broadest sense to indicate an antireductionism that is not just in opposition to a reductionist program, but also proposes a positive alternative.
5. For further hints see comments on Haldane’s fusion of biochemistry and genetics (Caspari, 1968, p. 43); his synthesis of findings from various biological disciplines (Wright, 1968, pp. 1, 3); his multilevel thinking (Pirie, 1968, p. 257); and Dronamraju’s general claim that Haldane was “a great synthesizer” (Dronamraju, 1968, p. vii).
6. For Haldane’s increasing sympathy to materialism, see Haldane (1937c [1932], pp. 247–249; 1937b [1932]; 1937e [1932], pp. 155–156; also discussed in Hammond [2004, pp. 73–91] and differently by Sarkar [1992b, pp. 394–396]).
7. Other authors have assumed that Haldane accepted dialectical materialism at the time of his political conversion to Marxism in 1937 (Sarkar, 1992b, pp. 398–399; Shapiro, 1993). I argue it occurred before 1937 (Hammond, 2004, pp. 79–91).
8. A striking example is Haldane’s explanation near the end of his life for writing a poem about the rectal carcinoma that would finally kill him: “I am a good enough Marxist to think that every poem should have a social function, though not a good enough one to think that it must. The main functions of my rhyme . . . [are to] . . . induce cancer patients to be operated on early and to be cheerful about it” (Haldane, as quoted in Clark, 1968, p. 258; see also Haldane, 1961, p. 32). On his confusion: “A few centuries of Stalinism or technocracy might be a cheap price to pay for the unification of mankind” (Haldane, as quoted in Adams, 2000, p. 487).
9. The ensuing comments apply only to the English variant of this debate and derive, in large measure, from exchanges in *Nature*. See Hammond (2004, pp. 56–63, 71–79).
10. The terminology describing antireductionist positions in this period varies widely. J. S. Haldane denied being a vitalist, associating this term with those who proposed a distinct vital substance, and referred to his own position as “organicism.” For my purposes, I refer to J. S. as



- a “vitalist” because he insisted on a distinct biological category that could not be investigated by physicochemical means. For short accounts of J. S.’s position, see J. S. Haldane (1908); Anonymous (1919). For a detailed analysis see Sturdy (1987, 1988).
11. Among others who developed an antireductionist and antivitalist program were Joseph Needham, the embryologist and philosopher of biology Joseph Henry Woodger, and Conrad Hal Waddington. On Needham and Woodger see Abir-Am (1987); Haraway (1976, pp. 101–146); Yoxen (1986, pp. 316–318). On Needham see Abir-Am (1991) and Needham (1932). On Woodger see Woodger (1929; 1930, pp. 1–22) and Yoxen (1986, pp. 314–315); on Waddington see Waddington (1929; 1931) and Yoxen (1986).
  12. From as early as eight years old J. B. S. was directly involved in his father’s physiological experiments. The only other period in which J. B. S. performed physiological research was during World War II. For accounts of J. B. S.’s physiological work, see Clark (1968, pp. 17–19, 27–29, 58–62, 135–151); Dronamraju (1968); Haldane (1932d, 1927); Pirie (1966, pp. 234–235); and for J. B. S. on J. S.’s physiological work, see Haldane (1961).
  13. On Hopkins as holist see Kamminga and Weatherall (1996). Although the quotes used are not from Hopkins’s pronouncements in the 1920s, when Haldane learned how to do Hopkins’ biochemistry, I have chosen them for their concision. They illustrate aspects of Hopkins’ position that remained fairly constant in the 1920s and 1930s. For useful summaries of Hopkins’ position see Hopkins (1949c [1927] and 1949b [1936]; see also Hopkins, 1931, 1932a, 1932b, 1949a [1932], 1933a, and 1933b).
  14. Other philosophically inclined biologists of the 1920s were also interested in Whitehead’s ideas. This included Haldane’s associates the evolutionist Conrad Hal Waddington and the embryologist Joseph Needham (Needham, 1931, p. 29; Needham, 1943b; 1941; Waddington, 1929; Waddington, 1975, p. viii). Joseph Woodger was also inspired by Whitehead (Woodger, 1930, p. 7). Ambiguity in Whitehead’s writings also allowed the vitalists who opposed Hopkins’s views to claim the former as support for their own position (for example, Russell, 1934, pp. 835–837).
  15. This was also true for Haldane later on. See Haldane (1941, p. 43; 1948, p. 3).
  16. This is not to say Haldane omitted biochemical arguments in his studies of allelomorphous series prior to 1931. In 1927 he used a biochemical argument to support the quantitative concept of allelomorphous series. He suggested certain work by Wright could be explained by the biochemical environment of allelomorphs constraining their activity—strictly speaking, the activity of enzymes as the primary products of these allelomorphs (Haldane, 1927c, p. 201). However, this biochemical argument was used within the *atomistic* context of the question of the quantity of primary product (that is, enzyme) being “produced” from the allele. In a similar manner, Haldane argued that Fisher’s theory of dominance could only apply to a limited number of cases (Haldane, 1930b). Haldane appears to have discarded this particular criticism of Fisher’s theory after 1930, about the same time he dispensed with his atomistic approach in general.
  17. On the latter, he acknowledged a debt to Gavin de Beer’s *Embryology and Evolution* (1930) (Haldane, 1932g, p. 16). Haldane’s interest in embryology certainly predated 1932. He must surely have discussed it with his associates and embryological researchers Joseph Needham and Conrad Hal Waddington (for examples of the interconnections between the three scientists on embryology see Haldane (1941, p. 197) and Yoxen (1986, pp. 313–315). Others were also interested in the issue of gene action in the early 1930s, but few had ideas on the topic with the level of sophistication found in Haldane’s paper (Allen, 1978, pp. 298–301; Keller, 2000, pp. 75–76; Provine, 1986, pp. 301–302; Wright, 1934; Zeleny, 1933).
  18. Haldane had been using the analogy of the gene as an organ from at least 1920 (Haldane, 1920, p. 8; Hammond, 2004, p. 167), but this is possibly the clearest exposition of its meaning for him.
  19. *Mathematical Theory* paper 6 was “Received 12 February, read 24 February, 1930” (Haldane, 1930a, p. 220). *Mathematical Theory* paper 7 was “Received 12 November, read 8 December, 1930” (Haldane, 1931b, p. 131). *Mathematical Theory* paper 8 was “Received 20 November, read 8 December, 1930” (Haldane, 1931c, p. 137). All emphases are in the originals.

20. Further evidence for Haldane's mechanistic approach to genetics in the 1920s being a short-term tactic was his awareness during this period of the need to move to considerations of the internal differentiation of these entities: "Just as the internal structure of atoms was elucidated by physicists rather than chemists, it is probable that the inner nature of the gene is a problem for the biochemist rather than the geneticist . . . how the genes cooperate in development, is analogous to the problem of how atoms cooperate in a molecule" (Haldane, 1927d, p. 456).
21. Haldane's account of Bidder's cataclams was based on the version found in *Nature* of Bidder's paper read to the Linnaean Society (Bidder, 1930; Haldane, 1931b, p. 135). There is evidence that other holists among Haldane's close colleagues were interested in Bidder's theory, such as J. D. Bernal and Joseph Needham (Bernal, not dated). Haldane also attributed a similar ecological argument to Ridley (1905) concerning plants and Elton (1927) for animal species (Haldane, 1932f, pp. 118–119).
22. Bidder's example of a cataclasm concerned sponges living in the littoral zone (the coastal area between high and low tides). Haldane referred to floods sweeping "large numbers of normal-eyed aquatic animals into a cave where the majority are blind" (Haldane, 1930a, p. 229; see also Haldane, 1932f, pp. 117–118).
23. This was also the first occasion, based on Bidder's theory, that Haldane felt there was an explanation for apparently nonadaptive features, for "apparently useless characters which nevertheless have been selected for their own sakes, for an entirely different reason" (Haldane, 1932f, p. 117).
24. In *The Causes of Evolution*, Haldane again mentioned how "two genes one at a time produce a disadvantageous type, but taken together are useful" (Haldane, 1932f, p. 100) and "Gonzalez" work was the example again.
25. I use the term "dialectical materialism" because it is still the best phrase to express the Marxist philosophy espoused by Karl Marx, Friedrich Engels, Vladimir Lenin, and Leon Trotsky. The term has a history before and after the Stalinist era and should not be conflated with the Stalinist "diamat" (see Rée, 1984, pp. 2–3, 134–135n6; and Sewell & Woods, 1983). The degree to which Haldane's early usage of dialectical materialism may have been influenced by Stalinized "Leninism" requires further investigation.
26. See also Bell and Haldane (1937) and Haldane (1938, pp. 73–74).
27. On Needham's partial adoption of dialectical materialism, see Blue (1998).
28. His first use of this concept was in his dialectical materialist model of the phenomenon of mind (Haldane, 1934, pp. 87–88).

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