Perspectives

Anecdotal, Historical And Critical Commentaries on Genetics

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LANCELOT HOGBEN, 1895–1975

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LANCELOT HOGBEN, whose birth centennial was last December, was one of the most versatile biologists of his generation. In genetics he made methodological contributions to human and medical genetics and provided an analysis of the nature-nurture dispute that was influential in its time. In zoology he was a pioneer of comparative (and evolutionary) physiology. He helped found the Society for Experimental Zoology. He invented what was, for 15 years, the standard pregnancy test. He made significant contributions to medical statistics in the United Kingdom and drew on that experience to write an incisive philosophical work on the foundations of statistics. He wrote four books on linguistics.

Although overshadowed by J. B. S. HALDANE, HOGBEN was like him in being one of the most successful popularizers of science of his generation. One of his books, *Mathematics for the Million* (HOGBEN 1936), went through four editions and sold more than half a million copies during his lifetime. It was translated into fifteen languages and remains in print. In his early years, he was a self-proclaimed socialist; in later years he called himself a scientific humanist. During World War I he was briefly imprisoned as a conscientious objector. Under the influence of his first wife, the mathematician ENID CHARLES, he was an active feminist. In the 1920s, unlike some geneticists, he did not succumb to racial prejudice. During a stay in South Africa (1927–30), he actively fought racial prejudice and discrimination to such an extent that he felt compelled to leave.

Childhood and education: LANCELOT THOMAS HOGBEN was born in the Portsmouth suburb of Swansea on 9 December 1895, two months prematurely. His father, THOMAS HOGBEN, was a fundamentalist (Plymouth Brethren) evangelist. His mother, MARGARET ALICE HOGBEN (*neé* PRESCOTT), was similarly religious—HOGBEN's "miraculous" premature birth prompted her to vow that he would be a medical missionary. In an intellectually austere family environment, made more austere by poverty, HOGBEN was brought up with that end in mind. He was encouraged to read secular textbooks of botany and zoology. These helped him develop a scientific interest in biology independent of the missionary hopes of his parents.

In 1905 the HOGBENs moved to London. HOGBEN attended Tottenham County School, where he pursued biology systematically and demonstrated exceptional academic abilities. He struck up many friendships with working-class boys of the neighborhood. This began a lifelong left-wing political orientation. At 16 he passed the University of London's External Intermediate Examinations. At 17 he became the first student from a London County Council secondary school to win a scholarship to Cambridge (Trinity College). In later life, when eugenists such as L. DARWIN attacked these scholarship schemes for allegedly being dysgenic and a waste of public resources (because students from poor families were genetically inferior), HOGBEN would remember his origins and rise to their defense.

By the time HOGBEN arrived at Cambridge in 1913, he had already graduated from the University of London. He found Cambridge intellectually stimulating and learned much from the physiologists W. M. FLETCHER, A. V. HILL, and K. LUCAS. He was influenced by BERTRAND RUSSELL, who was lecturing at Cambridge, especially on the philosophy of science. An additional influence were the writings of A. R. WALLACE, co-discoverer of natural selection and also an avowed socialist. HOGBEN's first significant publication, in 1918, was a journalistic account of WALLACE's life and work. During his Cambridge period HOGBEN became convinced that he would pursue a career in science instead of medicine. Socially, HOGBEN found Cambridge decrepit. Though he was an active member of the (left-leaning) student Fabian Society, which he moved further to the left, HOGBEN otherwise found it difficult to associate with the generally upper-class Cambridge students or to appreciate their predominantly extracurricular interests.

In 1914 HOGBEN found himself opposed to World

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War I. By this point he had fulfilled his academic requirements for a degree. He was left with only his residency requirements, which could be satisfied through war service. HOGBEN volunteered for noncombatant roles in two Quaker organizations. However, when conscription was introduced in 1916, he chose not to use this work to exempt himself from military service. Rather, encouraged by RUSSELL's public pronouncements on the issue, he returned to Cambridge and refused to serve on conscientious grounds. During his subsequent interrogation, he refused to be medically examined or to appeal to religious convictions. He was imprisoned but discharged on medical grounds before the completion of his initial three-month sentence. His convictions remained unchanged. When RUSSELL was himself imprisoned, HOGBEN wrote to him, "I am writing . . . to tell you how splendid I think your stand has been. Being an ex-convict I understand a little at what cost you have been true. It is inspiring to us who are younger men and who see so many of our friends succumbing to cynical indifference or academic preoccupation to know that there is at least one of the Intellectuals of Europe who have not allowed the life of the mind to kill the life of the spirit" (RUSSELL 1968, p. 83).

Early professional career: After his release, HOGBEN barely supported himself in London through journalism. In 1917 he was appointed a lecturer in zoology at Birbeck College. During this period he met ENID CHARLES, an organizer for the women's wing of the Trade Union Movement. CHARLES had a degree in mathematics, economics, and social sciences from Liverpool and was a committed feminist and socialist. They began living together almost immediately and were married shortly before the birth of their first child. HOGBEN moved to Imperial College in 1918 and wrote his only paper on paleontology (HOGBEN 1919). He attended the mathematical lectures of H. LEVY and developed his mathematical competency. In 1920 and 1921 he published six papers on experimental cytology, which earned him a D.Sc. from the University of London. His most important result was that cockroach chromosomes exhibited parasynapsis, rather than telosynapsis as was then generally believed (HOGBEN 1920a,b). This observation provided support for the MORGAN school's model of linkage and crossing over (WELLS 1978).

This cytological work led F. A. E. CREW to offer HOGBEN a position at the new Animal Breeding Research Laboratory in Edinburgh. However, HOGBEN's research had shifted to comparative endocrinology, which is what he pursued at Edinburgh. He studied the role of internal secretions in amphibian metamorphoses and color changes. HOGBEN (1923) was the first to describe hypophysectomy by the ventral approach (WARING 1963). His primary interest remained evolutionary and comparative. *The Pigmentary Effector System* (HOGBEN 1924) reviewed what was known about color changes in all groups of animals. HOGBEN and WINTON (1924) and HOGBEN (1926, 1927a) published systematic reports of these comparative studies. During this period, HOGBEN, HALDANE, JULIAN HUXLEY, and CREW founded the *Journal of Experimental Biology* and the Society for Experimental Biology to back the new journal (WELLS 1976). Financial support for the journal came partly from H. G. WELLS.

In 1925, HOGBEN left Edinburgh for Montréal to become Assistant Professor of Medical Zoology at McGill University. The post was short-lived. He left for South Africa in 1927 to his first appointment to a Chair (in zoology) at the University of Cape Town. HOGBEN's major innovations were to introduce experimental work in the department and to replace samples from the United Kingdom with local fauna. Outside the university he lectured to school teachers who were being trained in biology. Out of these lectures emerged *Mathematics for the Million* (HOGBEN 1936), his most popular book. In his research he concentrated mainly on Xenopus, particularly *Xenopus laevis* (the clawed toad). HOGBEN noted that female *X. laevis* laid eggs after being injected with anterior pituitary extract. CHARLES collaborated in this work (HOGBEN *et al.* 1931). At that time the active hormone in this extract was believed to be identical to the gonadotrophic substance in the urine of pregnant women (WELLS 1978). After protocols for maintaining reproductively healthy *X. laevis* stocks in the laboratory were worked out, in HOGBEN's laboratory and elsewhere (see LANDGREBE 1939), this observation led to what CREW (1939) named the "HOGBEN pregnancy test."

Except for the Montréal interlude, HOGBEN remained politically active throughout this period. In London he tried left-wing labor organizing. In Edinburgh he hosted meetings of the students' Socialist Society. In Cape Town he was confronted by the racism that eventually led to apartheid. Many years later, in *Dangerous Thoughts,* HOGBEN (1939b) recorded that there was a universal consensus among South African whites, even in relatively liberal Cape Town, about the racial inferiority of Africans, Coloureds, and Indians. "Chromatocracy" was his description of South Africa. In his classes, and in his social life, he challenged the chromatocracy. In *Principles of Evolutionary Biology* (HOGBEN 1927b), based on his classroom lectures, he extensively quoted MORGAN (1925) and BATESON (1913) on the fallacy of assuming the genetic superiority of one race over another. He dismissed eugenics, claiming that it had "no enthusiastic supporters among the leading investigators in genetics" (HOGBEN 1927b, p. 100). He admitted colored students in his classes and welcomed them to his home. South African whites did not appreciate this racial apostasy. By 1929 HOGBEN felt uncomfortable in South Africa. It was lucky for him that, right at this juncture, the London School of Economics (LSE) created a new Chair of Social Biology. HOGBEN was appointed to it in 1930.

By this time, HOGBEN's basic philosophical views were set. As a physiologist in the 1920s, just like J. B. S. HALDANE (see SARKAR 1992a), HOGBEN was accosted by a dominant holist epistemology, barely different from "vitalism" and propounded most forcefully by HALDANE's father, the physiologist J. S. HALDANE. HOGBEN (1930) provided a vigorous defense of mechanistic explanation. However, he separated the private from the public sphere—scientific questions, as well as issues of metaphysics and epistemology, occurred only in the latter. Religious and political beliefs, ethical commitments, and aesthetic preferences, all belonged to the former. The main function of this distinction was that it permitted HOGBEN to declare the ethical neutrality of science. HOGBEN rejected eugenics because it violated this distinction; moreover, in the private sphere of politics and ethics, it was offensive to his egalitarian principles. However, this left open the pursuit of a value-neutral human genetics that could potentially be put to medical and social use. This is the task that he set for himself in his new position at the LSE.

Human genetics: R. A. FISHER was among those over whom HOGBEN was preferred for the Chair at LSE (see BENNETT 1983, pp. 112–113). Ironically, when HOGBEN turned to human genetics as a way of fulfilling the mandate of his new position, it was FISHER's seminal work that provided the point of departure. *Genetic Principles in Medicine and Social Sciences* (HOGBEN 1931b) summarized his agenda. It was a critical look at the practice of human genetics up to that point. The first chapter gave a careful analysis of twin studies, how they can reveal genetic origins of phenotypic differences, and how they are prone to misinterpretation by both sides in the nature-nurture dispute. The second chapter attempted a rigorous treatment of segregation analysis. The sixth chapter contained the first systematic account of HALDANE's work on selection in the 1920s, which FISHER (1930) had completely ignored (SARKAR 1992b). However, the third chapter was the most important. It drew attention, for the first time to an English-speaking audience, to the important work done by BERNSTEIN (1931) on the detection of linkage (MAZUMDAR 1992). Let *Aa Bb, aa bb, etc.*, represent the frequencies of the genotypes in a two-locus/two-allele model (*A* and *a* are the alleles at the first locus, *B* and *b* at the second). Bernstein had invented the statistic $y = (Aa\ Bb + aa\ bb)(Aa\ bb + aa\ Bb)$, which does not depend on the linkage phase (*cis* or *trans*), but increases monotonically with the recombination fraction, in order to detect linkage from the mating $Aa\ Bb \times aa\ bb$ (see CROW 1993). The invention of this statistic was a crucial step in human linkage studies—HOGBEN had immediately recognized its importance.

The last two chapters, as HOGBEN clearly indicated, were political rather than scientific. HOGBEN's implicit target was the controversial last chapters of FISHER's (1930) *Genetical Theory of Natural Selection*. The same topics were treated but, whereas FISHER emphasized heredity and pushed for eugenics, HOGBEN attempted to dissect hereditarian claims. He opted for social renewal and continued his campaign against eugenics. The suggestion of LEONARD DARWIN (1926), CHARLES DARWIN's son, that scholarships to poor children be discontinued because they were obviously dysgenic met with particular scorn—HOGBEN was clearly recalling his own origins. The book was well received and, during the 1930s, was probably HOGBEN's most influential work (MAZUMDAR 1992). In *Eugenics Review*, HUXLEY (1932), though extremely critical of HOGBEN's anti-eugenic ideas, nevertheless commended the book as "an important contribution to human biology, and one which it will be extremely salutary for eugenists to read." In *Nature*, HALDANE (1932) opined that "Hogben's book is at least the herald of a more scientific epoch" of human genetics. Needless to say, DARWIN was less pleased. "I . . . should enjoy giving him one in the eye!!" he confided to FISHER in a letter (29 March 1932; see BENNETT 1983, p. 153).

Much of HOGBEN's work on mathematical human genetics consisted of extensions of methods discussed in *Genetic Principles*. HOGBEN (1931a, 1932a–c) developed more rigorous methods for segregation analysis. HOGBEN *et al.* (1932) used these methods to establish, rigorously, the dependence of alkaptonuria on a single recessive gene, which GARROD (1902) had suggested immediately after the rediscovery of MENDEL's laws. HOGBEN (1932d,e) worked out the correlation of relatives for sex-linked inheritance, extending FISHER's (1918) classic treatment. CHARLES (1933) extended these results. HOGBEN (1934a,b) turned to the detection of linkage. He corrected and extended BERNSTEIN's (1931) analysis. HALDANE (1934) provided other extensions. In 1935, FISHER (1935) showed that maximum likelihood methods were more efficient than the *y* statistic. However, computing FISHER's *u*-scores was very laborious, as HALDANE and SMITH (1947) pointed out—instead, they applied LODs to linkage analysis (see MORTON 1995). Between maximum likelihood and LOD methods, BERNSTEIN's and HOGBEN's attempts are now only of historical interest.

HOGBEN's attempt to clarify and analyze the nature-nurture dispute, also initiated during this period, has been of more lasting interest. His basic argument was for the "relativity" (HOGBEN 1933a) or "interdependence" (HOGBEN 1933b) of nature and nurture. He emphasized the interaction of nature and nurture. While the calculation of correlation coefficients could be used to show the genetic or the environmental origin of differences in traits such as IQ (HERRMAN and HOGBEN 1933; HOGBEN 1939a), it could not be used to ascribe definite values to the relative importance of these factors. Such techniques (and all others that could be

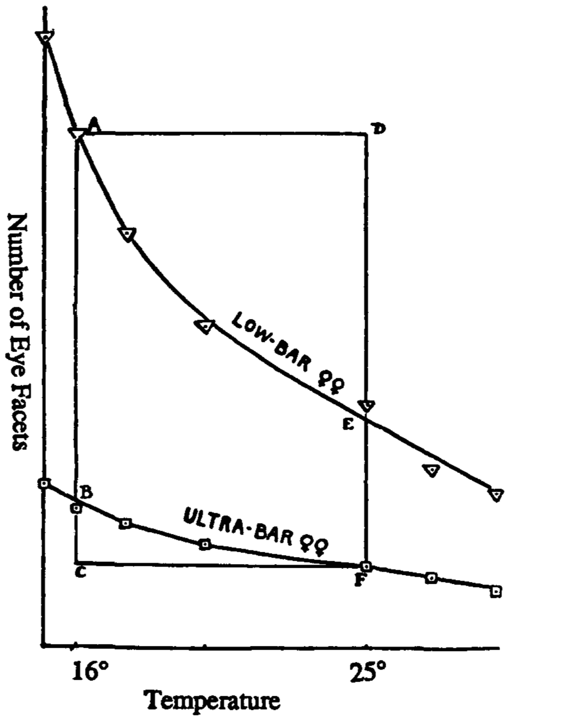

FIGURE 1.—Modified from HOGBEN (1933a, p. 384). The graphs, as indicated, are for the *low-Bar* and *ultra-Bar* genotypes. Ordinate, number of eye facets; abscissa, temperature during development. The data are from KRAFKA (1920). For a full discussion, see the text.

derived from the analysis of variance) were only quantitatively meaningful when relativized to a specified environment. Using KRAFKA's (1920) data on development in Drosophila, HOGBEN (1933a) drew a figure (see Figure 1) to show the interaction of nature and nurture. Two mutants, *low-Bar* and *ultra-Bar,* both have many fewer facets in the compound eye than the nonmutant. The graph shows the number of facets as a function of the temperature at which the strains were cultured. Assuming the same frequency (0.5) for both mutants, HOGBEN calculated the (total) phenotypic means and variances for facet numbers to be (120.5, 4692.5) at 15° and (49.5, 600.25) at 25°. Neither estimate is preferred, he argued, and this shows that it is unjustified to try to use these parameters to assign a quantitative value to genetic or environmental influences in general, independent of a specified environment. HOGBEN emphasized that situations similar to that depicted in Figure 1 were routine rather than exceptional.

This argument was repeated in *Nature and Nurture* (HOGBEN 1933b). Throughout his career, HOGBEN continued to devise better didactic methods for a recognition of nature-nurture interactions (see, *e.g.,* HOGBEN 1951). Though it eventually became standard, in the 1930s HOGBEN's argument was greeted by silence. HALDANE (1936, 1946) devised an alternative argument to demonstrate nature-nurture interaction. Even FISHER was circumspect. "I think I see your point now. You are on the question of non-linear interaction of environment and heredity," he wrote to HOGBEN (25 February 1933; see BENNETT 1983, p. 218). "[t]he main point is that you are under no obligation to analyze variance into parts if it does not come apart easily, and its unwillingness to do so naturally indicates that one's line of approach is not very fruitful."

However, to J. A. F. ROBERTS, FISHER wrote more confidently, "There is one point in which Hogben and his associates are riding for a fall, and that is in making a great song about the possible, but unproved, importance of non-linear interactions between hereditary and environmental factors. J. B. S. Haldane seems tempted to join in this" (18 January 1935; see BENNETT 1983, p. 260). Over 60 years later, for human traits, the dispute remains unresolved. (Graphs showing nonlinear interactions are routinely found for many traits in animal populations. However, because of the obvious experimental difficulties, any such graphs are not only not available for human populations, but nature-nurture interactions have proven difficult to detect.)

Medical statistics: In 1936 HOGBEN was finally elected to the Royal Society. In 1937 he left LSE to become Regius Professor of Natural History at the University of Aberdeen. Though he continued some of his work in endocrinology, from this point on any active interest in genetical research seems to have waned. It was replaced by a newfound interest in linguistics, which continued for the rest of his life. In March, 1940 HOGBEN went to Norway to lecture on Nazi theories of racial superiority. While he was there, Germany invaded Norway. HOGBEN and his daughter escaped to Sweden, but were unable to return to the United Kingdom by any direct route. They flew to Moscow, crossed the Soviet Union on the Trans-Siberian Railway, and traveled by ship to Japan and finally to San Francisco. The trip reinforced HOGBEN's dislike for the Soviet Union, but, strangely, largely on aesthetic grounds (HOGBEN 1940).

HOGBEN's family assembled in America. CHARLES was already working in Ottawa; their eldest son, ADRIAN, was a student at the University of Wisconsin. HOGBEN accepted a one-semester Visiting Professorship there and lectured on mathematical genetics. These lectures were eventually published as *An Introduction to Mathematical Genetics* (HOGBEN 1946). It included what was then the most detailed discussion of the problem of relating theoretical results (such as the Hardy-Weinberg ratios) with population data. Those in his class were impressed by his convivial manner, his personal interest in his students, and his ability to present mathematical arguments in a clear and easily comprehensible way. The Wisconsin appointment provided HOGBEN with sufficient funds to return to the United Kingdom; CHARLES remained in Canada. Back at Aberdeen, he was irritated by suggestions that he had not returned there as soon as possible. In any case, his laboratory staff had been dispersed by World War II, and HOGBEN left in 1942 to become Professor of Zoology at the University of Birmingham.

At Birmingham, HOGBEN studied comparative temperature regulation in mollusks, earthworms, amphibians, and reptiles (HOGBEN and KIRK 1944; KIRK and HOGBEN 1946), as well as sensory responses in Drosophila (BEGG and HOGBEN 1946). He also continued writing political tracts. However, his health deteriorated owing to thyroid problems, and he underwent thyroidectomy in 1943. After a partial recovery, he began war work under CREW (while refusing to wear a uniform). Most of his work was statistical and consisted of a revision of army medical documentation followed by therapeutic trials. An important result was a demonstration that indiscriminate prophylactic use of antibiotics leads to the selection of resistant strains of disease-causing microorganisms (WELLS 1978). To publicize the work that emerged from these statistical studies, the *British Journal of Social Medicine* was founded by the British Medical Association, with HOGBEN as its first Editor.

After the war, HOGBEN continued work in medical statistics, though with less success. Perhaps the most important offshoot of this work was his searching examination of the foundations of statistical theory (and practice), which remains relevant today. HOGBEN (1957) was skeptical of the mathematical basis for the methods for inference introduced by FISHER, while also doubting the NEYMAN-PEARSON methods and WALD's decision theory (WELLS 1978). However, he had no alternative framework to present. Meanwhile, his marriage had ended. In 1947 CHARLES had returned from Canada, but she and HOGBEN never readjusted to living together after their six-year separation. In 1953 CHARLES left for East Asia. They were divorced in 1957 so that HOGBEN could marry SARAH EVANS, a Welsh school teacher and local political activist. After their marriage, they settled in Wales, where HOGBEN had bought a riverside cottage. Throughout this phase of his career, HOGBEN's most significant interest was in linguistics. *The Loom of Language* (BODMER 1944), which HOGBEN supervised, dealt with the evolution of language and proposed the creation of an auxiliary language for international communication. It sold over 130,000 copies (WELLS 1978).

Retirement: HOGBEN retired from the University of Birmingham in 1961. In 1963 the premier of British Guyana, C. JAGAN, invited him to become the Vice-Chancellor of a new University of Guyana. HOGBEN visited Georgetown for a month in 1963 and accepted the position. He reorganized the plans for the University to make it more directly responsive to local economic needs and interests (rather than being a liberal arts college affiliated with the University of the West Indies). He spent much of 1963 raising funds for the new university. For the 1963–64 academic year, HOGBEN served as Vice-Chancellor. However, an extended strike and political instability made his short tenure uncomfortable. After ensuring that sufficient financial support was assured to the University, he resigned in 1964.

Returning to Wales, HOGBEN continued his work on linguistic subjects. HOGBEN's *The Vocabulary of Science* (1969) is an analysis of scientific vocabulary in all European languages. He continued his popular scientific writing and prepared the fourth edition of *Mathematics for the Million* (1967). He also wrote some intriguing philosophical pieces. However, the last decade of his life (from 1965 to 1975) was unhappy. Both his and EVANS' health deteriorated progressively. EVANS died in 1974, after the ultimate failure of an earlier mastectomy to remove a malignant tumor. HOGBEN died on 22 August 1975.

HOGBEN lived a long and varied life. Like his more famous contemporary, HALDANE, he became involved in so many projects, scientific, social, and political, that his contribution to any one was diminished. As a result, there is no important finding by which we remember his name. Instead, we memorialize him for his breadth of interest, his lifelong commitment to social justice, and his not inconsiderable contributions to such diverse fields as social medicine, physiology, and genetics. He should also be remembered as a superb popularizer of science, one who could make scientific matters alive for any audience he chose. Mindful of his great emphasis on interactions, we can note that the totality of his contributions is not properly measured by summing the component parts.

No detailed scientific biography of LANCELOT HOGBEN exists. Biographical details for this piece were mostly gleaned from WELLS (1978), who provides personal information and a very useful chronology. WERSKEY (1978) provides an interpretation of HOGBEN's political development (along with those of J. D. BERNAL, J. B. S. HALDANE, H. LEVY, and J. NEEDHAM). The historical research on which this piece is based was partly funded by the National Institutes of Health (grant HG-00912).

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